ACTIVE MATTER

Sriram Ramaswamy

http://www.physics.iisc.ernet.in/~sriram

Centre for Condensed-Matter Theory

Department of Physics

Indian Institute of Science

Bangalore

NAG school Aug 2010

Lecture 1: Introduction & dry active matter

- What is active matter? why do we care?
- Particles and dynamical regimes, background
- From agents to continuum models
- Slow variables: conserved and broken-symmetry
- Polar flocks: theory and experiment
- Apolar flocks: theory and experiment

Lecture 2: Active particles in a fluid

- Active liquid-crystal hydrodynamics
- Inertial *vs* Stokesian mode structure
- Instabilities in various geometries
- Noise, active diffusion, fluctuation statistics
- Rheology of active ordered and isotropic phases
- Filament dynamics in an active medium

What is active matter?

- Active systems
  - Energy uptake → dissipate → motion

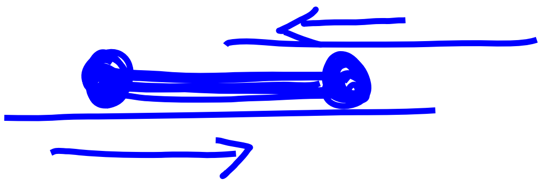
- Living matter is active
  - the cytoskeleton, or its extracts: motors filaments, ATP
  - the plasma membrane + pumps
  - whole living cells, all creatures great and small
  - dead imitations: catalytic nanorods, vibrated grains

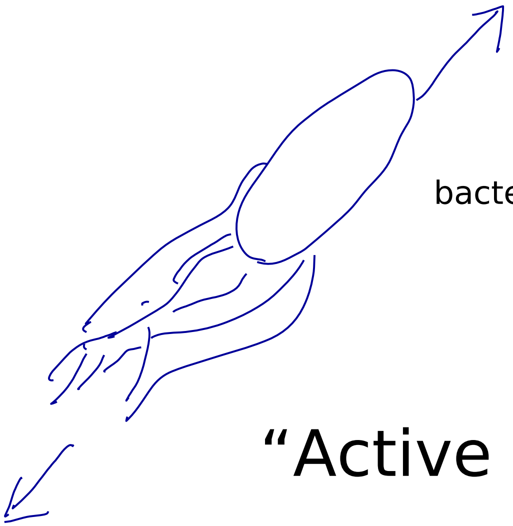
- Generic properties of living matter as a material?
  - mechanics and statistics

- Regimes:
  - In ambient fluid: hydrodynamic damping;
  - on a substrate: local friction

Active particles

Motor-filament complex





bacterium

“Active particles”

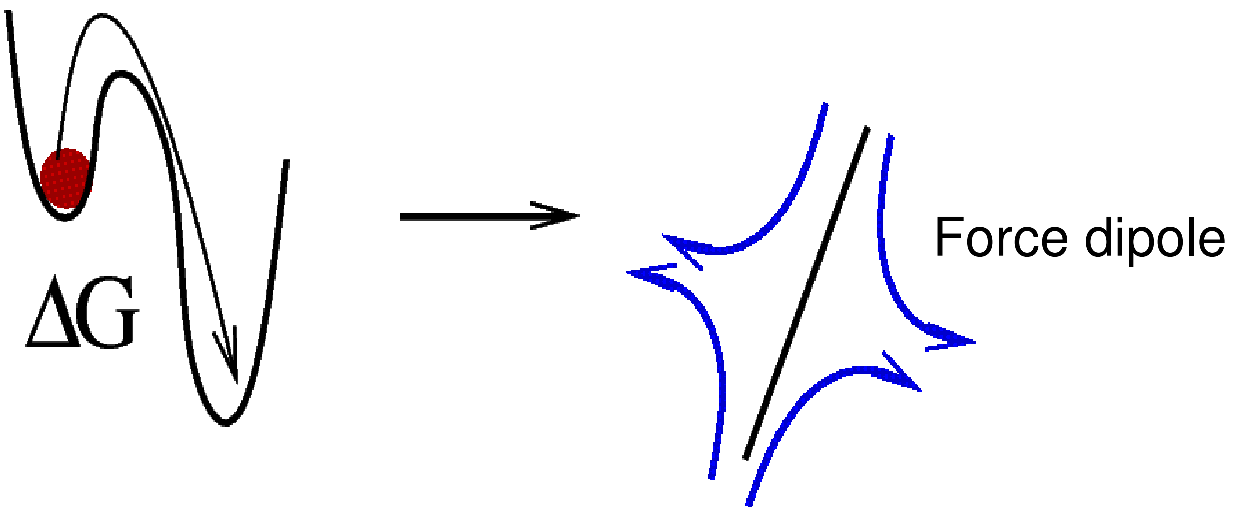
Chemical energy taken in

Internal coordinate cycles

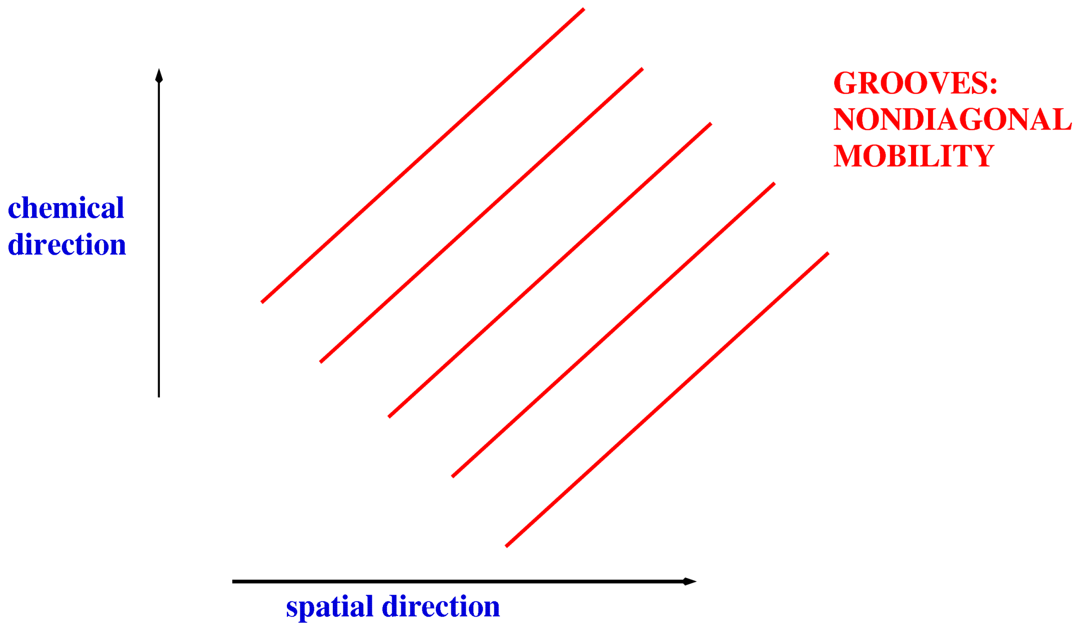
Energy dissipated – reaction products out

Particle translates, rotates, pulsates…

A minimal active particle



- Active particles consume free-energy
- Move and stir surrounding medium
- Require no *external* force

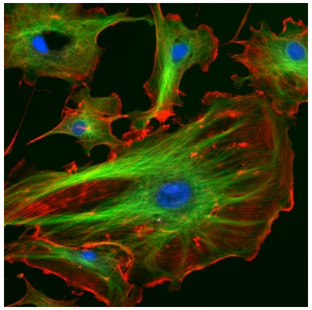


Motor: catalyst for fuel breakdown; 2d configuration space

Driving force **F** = $\Delta\mu$(ATP-ADP), in chemical direction

Mobility **M** nondiagonal

Motion **v** = **MF** has component in spatial direction

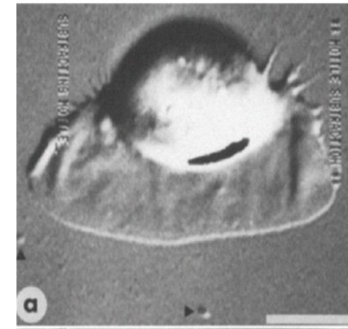


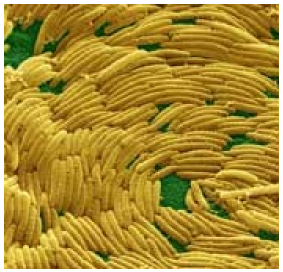
active cytoskeleton

http://commons.wikimedia.org/wiki/Image:FluorescentCells.jpg

lamellipodium

Small *et al.* J Cell Biol **129** (1995) 1275



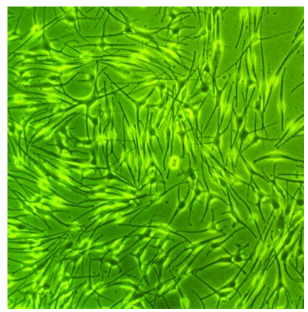


myxococcus

www.bio.indiana.edu/facultyresearch/faculty/Velicer.html

Melanocytes

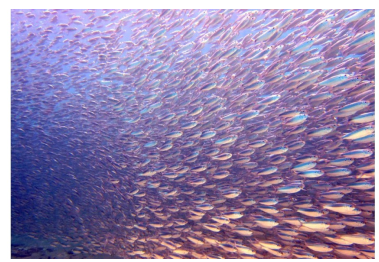
http://www.cellapplications.com/
products_image/FileCat000kyubvij.gif



Fish schools

www.flickr.com/photos/pmforster/496918483

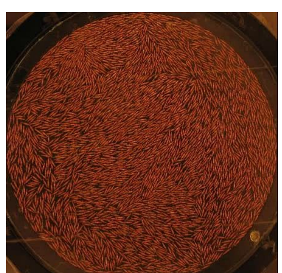
Why do we care?
Ubiquitous



Starling flock over Rome

http://angel.elte.hu/starling/

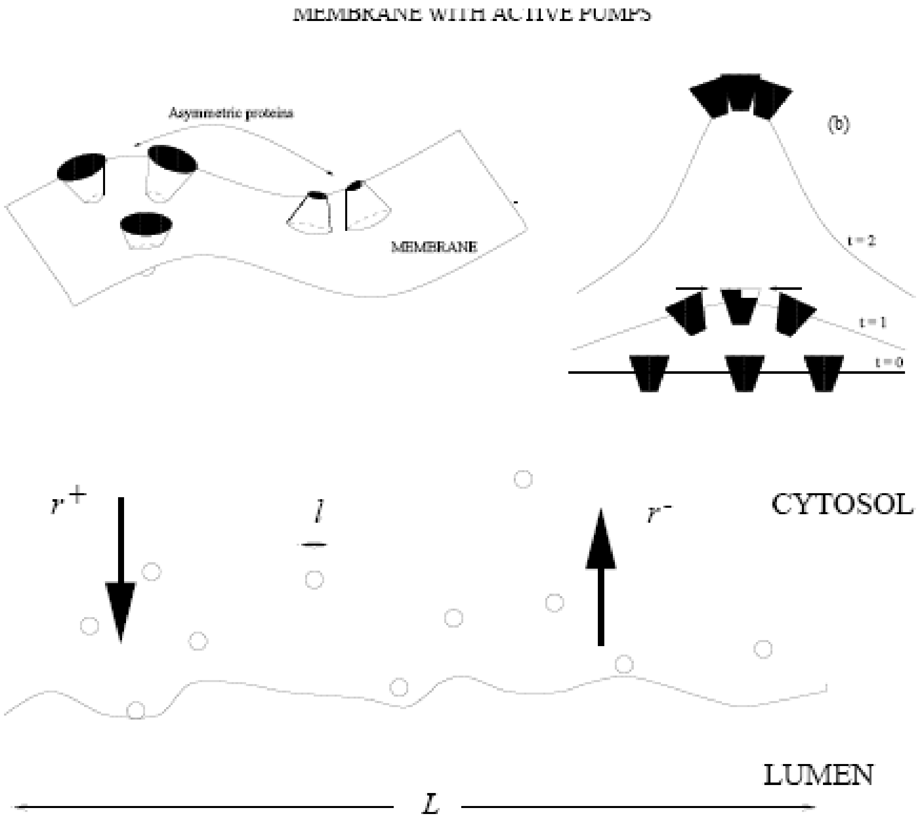
Dead active matter
Narayan *et al.* Science 2007



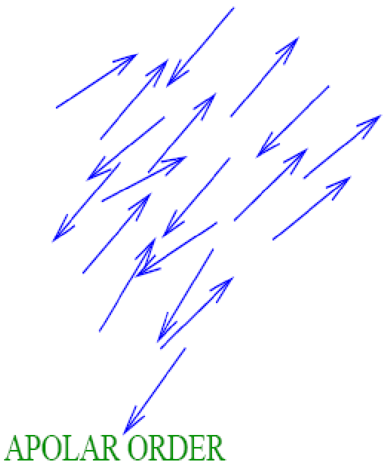
Active membranes

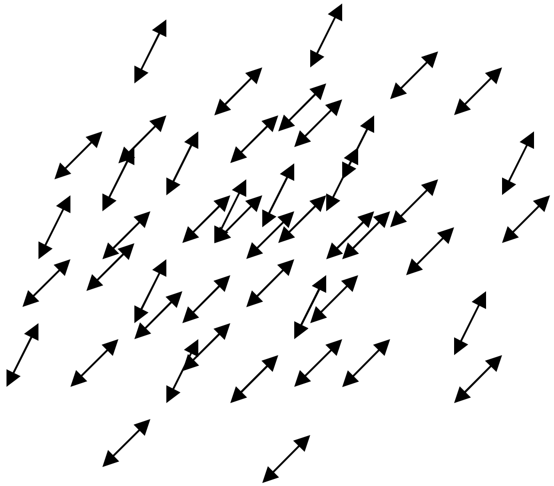
Not in this lecture

Prost & Bruinsma 1996
SR, Prost, Toner 1999
SR & M Rao 2001
Rao & Sarasij 2001
Bassereau et al. 2001-
Sankararaman, Rao, Kumar 2002



PARTICLES: APOLAR *vs* POLAR





fore-aft asym particles

can order symmetrically

Symmetric particles

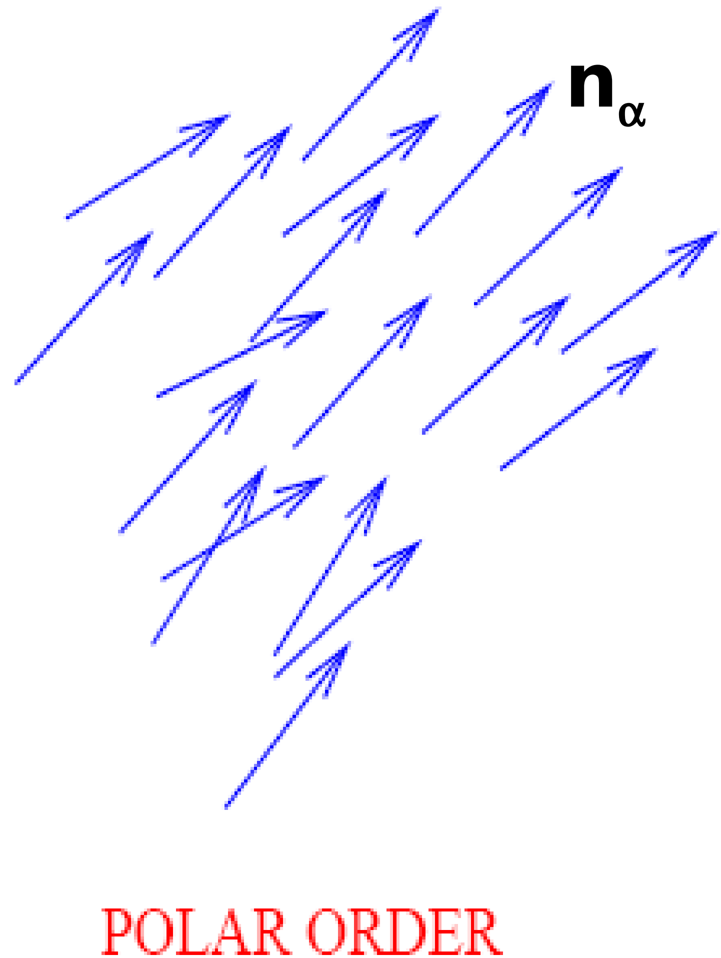
POLAR ORDER PARAMETER

$\mathbf{p}(\mathbf{r}) = \langle \mathbf{n}_\alpha \rangle$

$|\mathbf{p}|$: amplitude

$\mathbf{p}/|\mathbf{p}|$ = fixed-length spir

(*cf* XY model)



APOLAR ORDER PARAMETER

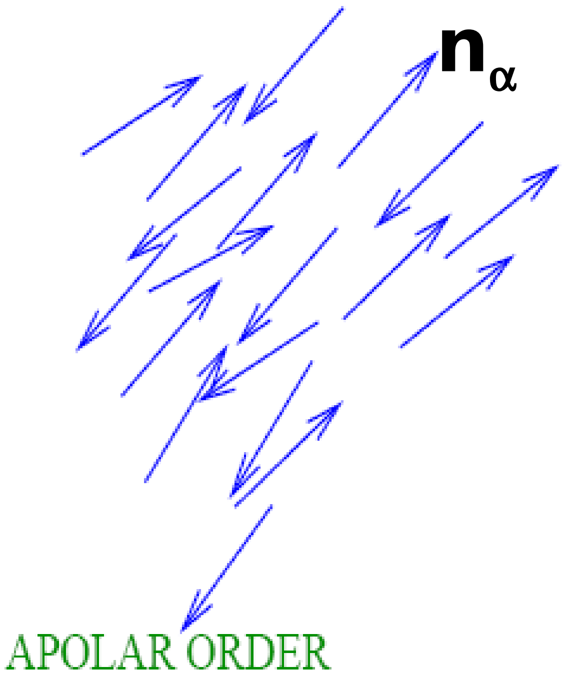
$\mathbf{Q}(\mathbf{r}) = \langle \mathbf{n}_\alpha \ \mathbf{n}_\alpha \ - \mathbf{I}/d \rangle$

d = dimension of space

||**Q**||: strength of order

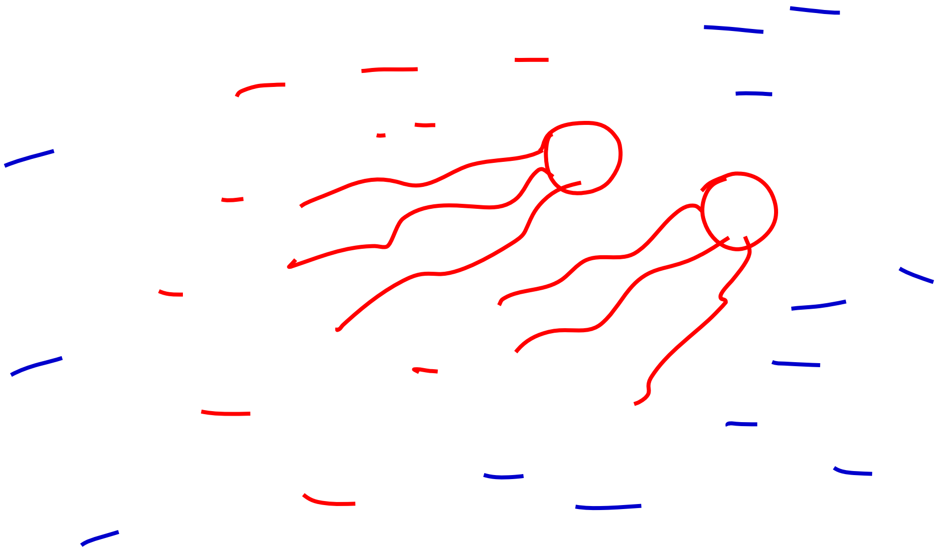
Principal axis = director

Q can be uni- or bi-axial



DYNAMICAL REGIMES

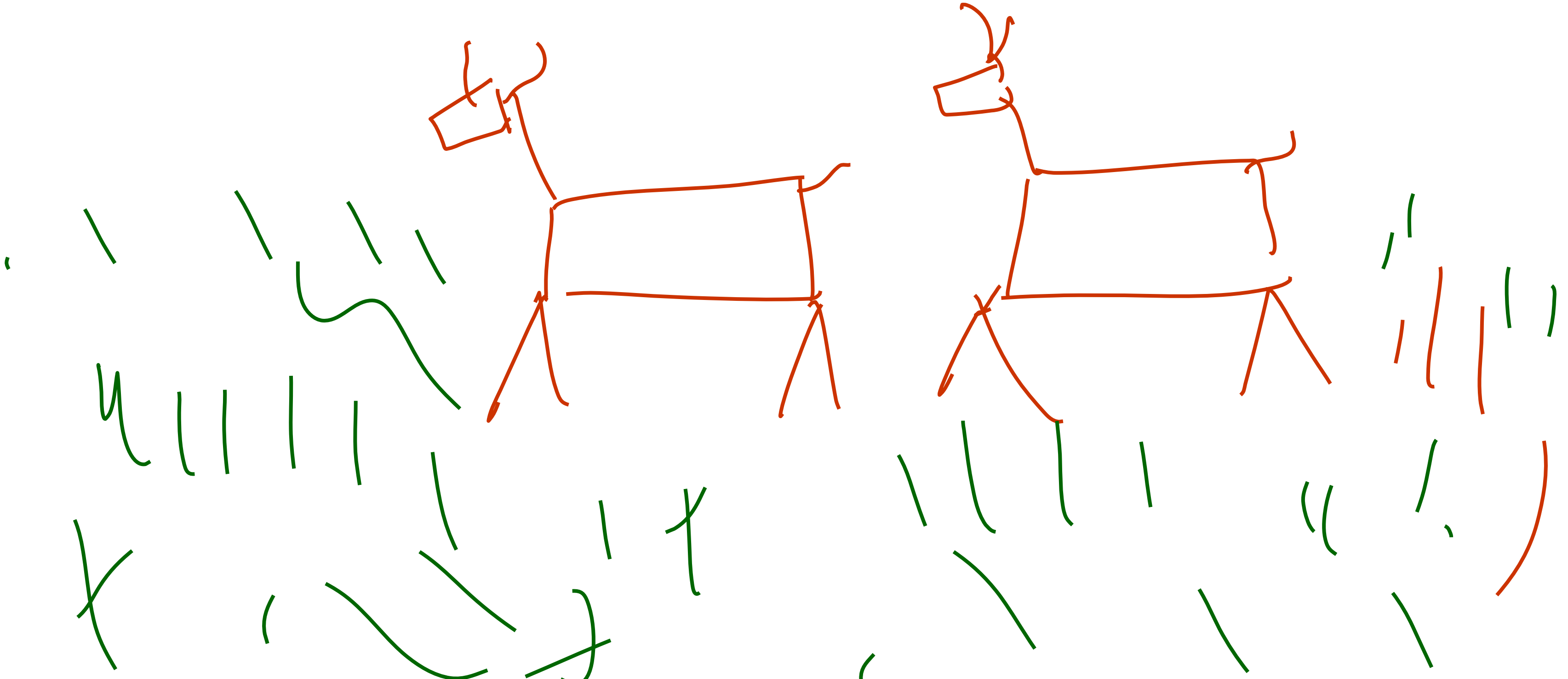
Suspension: hydrodynamic interaction



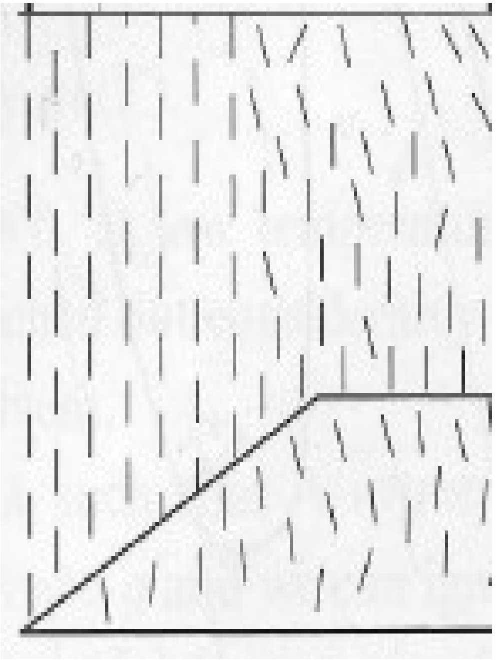
DYNAMICAL REGIMES

Substrate: passive friction, hydro flow killed

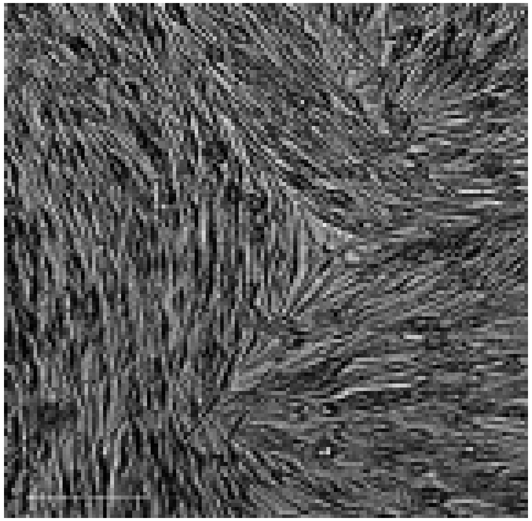
Confining walls: subtleties of incompressibility



How is active matter different?

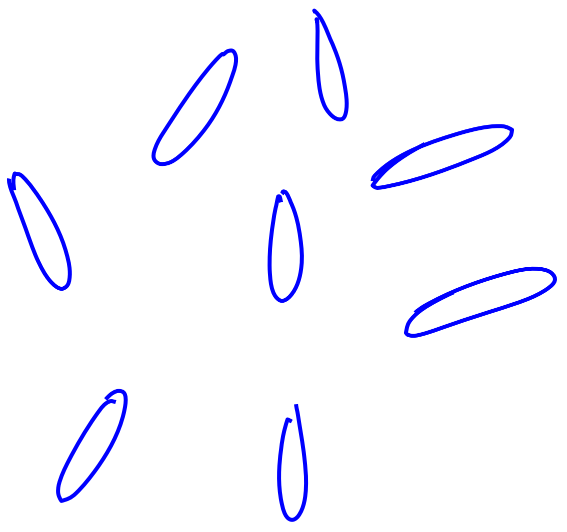


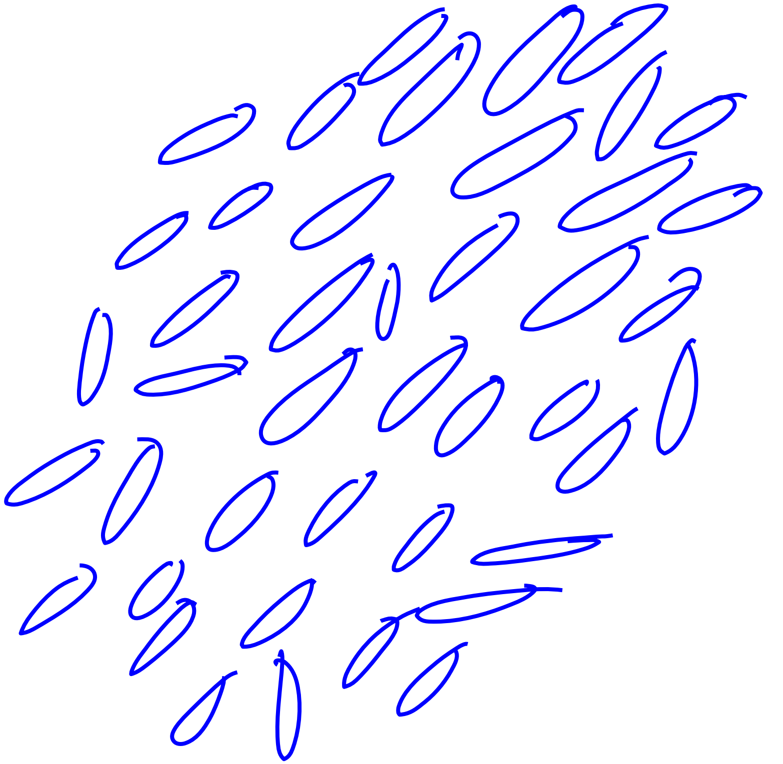
Dead brownian rods



Living cells

Won't answer the hard question





THERMAL EQUILIBRIUM, hard-particle systems

low conc → max ent isotropic   high conc → max ent nematic

STEADY STATE FAR FROM THERMAL EQUILIBRIUM

What rules decide how state is selected?

OUR APPROACH

Why do they form?

Mechanism of motion? HARD

ASSUME in or near ordered state

Response to disturbance? EASIER

Fluctuation statistics?

Coarse-grain: equations for slow variables

Short summary

Methods

- Flock = living liquid crystal
  - hydro variables: conserved, broken-symmetry
  - new stresses, currents, noise
  - thus build equations of motion
  - hence new modes, rheology, instabilities
- Relate hydrodynamics, microscopics
  - single-particle processes → stresses, currents
  - stochasticity → noise in coarse-grained eqns
- Experiments
  - Analogue system: granular monolayers
  - Bacteria, algal cells, cytoskeletal extracts

Broad message

Broken-symmetry hydrodynamics
and nonequilibrium statistical mechanics:

unifies mechanics of beasts, birds, bugs, cytoskeleton, catalytic nanorod swimmers, vibrated inelastic particles

Related work: many groups
Review articles:

- SR Annu Rev Condens Matt Phys 2010
- Toner, Tu and SR, Ann. Phys. (NY) 2005
- Kruse *et al.* Phys. Rep. 2007

A prescient paper

Convective instability by active stress:
B A Finlayson and L E Scriven,
Proc R Soc Lond A **310** (1969) 183

Concerned with living state
"gyrations of strands of living protoplasm"
But builds active stress from temp and conc gradients

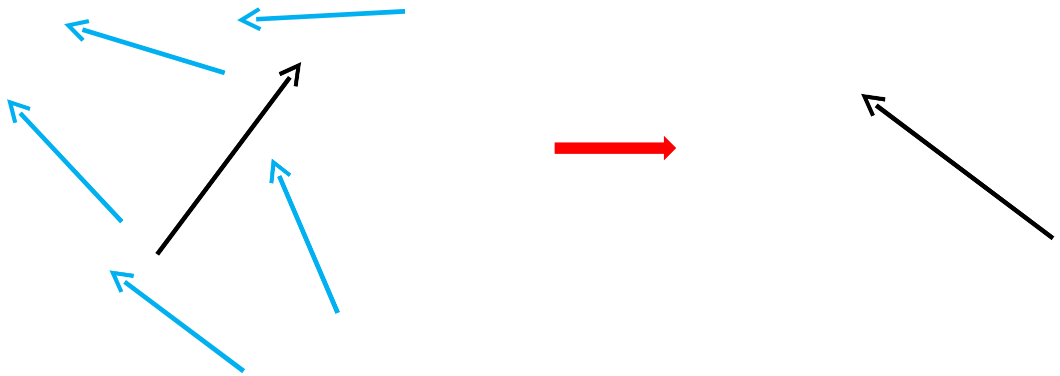
DRY ACTIVE MATTER

- Earlier work
- From particles to noisy PDEs
- active coarsening

Flock = active polar liquid crystal

- Reynolds 1987: movie stampedes
- Vicsek et al 1995: agent-based simulations
  - each particle: an arrow
  - orient parallel to neighbours + noise
  - move in direction of arrow
- Toner-Tu 1998: field theory
  - long-range order in $d = 2$

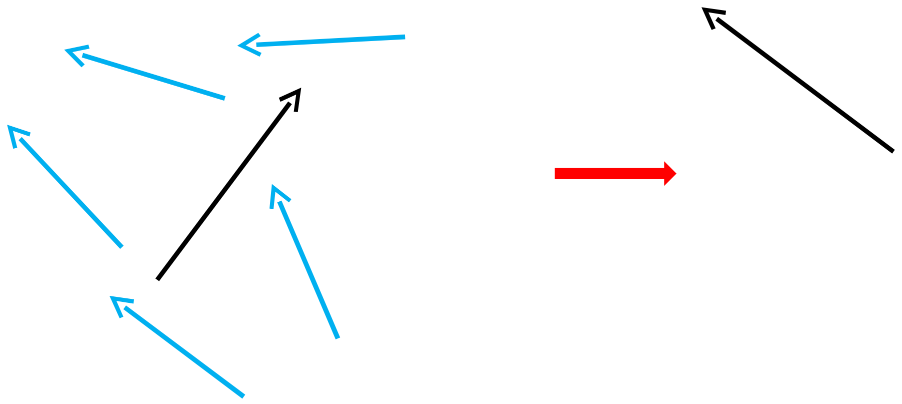
Interacting agents and flocking models



Each agent has position and direction
Aligns with mean of neighbours + noise

Reynolds 1987
Vicsek *et al.* 1995

Interacting agents and flocking models

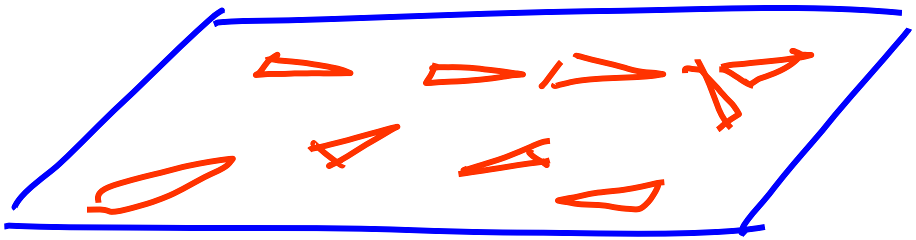


Each agent has position and direction
Aligns with mean of neighbours + noise
Follows its nose

Low noise, high density: ordered flock
High noise, low density: isotropic state
Reynolds 1987
Vicsek *et al.* 1995

Coarse-grain →

Continuum field theory: magnet or fluid?



Toner-Tu 1995, 1998

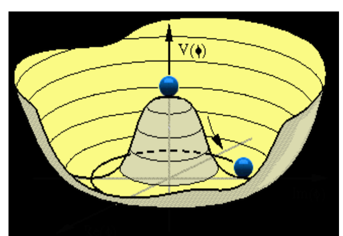
Orientation = velocity

Slow variables:
Conserved: conc field *c*
Broken sym: vel field ***p***

$$\partial_t c = -\boldsymbol{\nabla} \cdot c\,\mathbf{p}$$

$$\partial_t \mathbf{p} + \lambda \mathbf{p} \cdot \nabla \mathbf{p} + \ldots = (\alpha - \beta \mathbf{p} \cdot \mathbf{p})\mathbf{p} + \Gamma \nabla\nabla \mathbf{p} - \nabla P(c) + \mathbf{f}$$

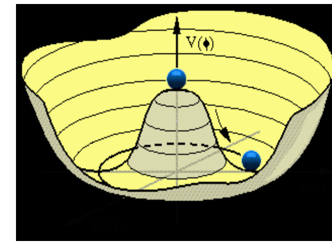
advection Preferred length alignment pressure noise



Derivation from micro:
Bertin et al 2003
Mishra 2009

http://www.hep.ph.ic.ac.uk/cms/physics/higgs-mecanisme.gif

In the ordered phase



small disturbances $\delta c, \delta \mathbf{p} \equiv (\delta \mathbf{p}_\perp, \delta p_{||})$

shift to a frame moving with speed p_0

$\delta p_{||}$ relaxes rapidly, so that on long timescales $\delta \mathbf{p} \simeq \delta \mathbf{p}_\perp$

$$\partial_t \delta c = -c_0 \nabla_\perp \cdot \delta \mathbf{p}_\perp \qquad \partial_t \delta \mathbf{p}_\perp = -P'(c_0) \nabla_\perp \delta c$$

$$\omega = \pm \sqrt{c_0 P'(c_0)}\, q_\perp$$

Ordinary sound rediscovered?
No, 1st sound comes from momentum conservation
This is a broken-symmetry mode

Fluctuations in the ordered phase

Include noise in equation for **p**
Fluctuations easily calculated in linear theory

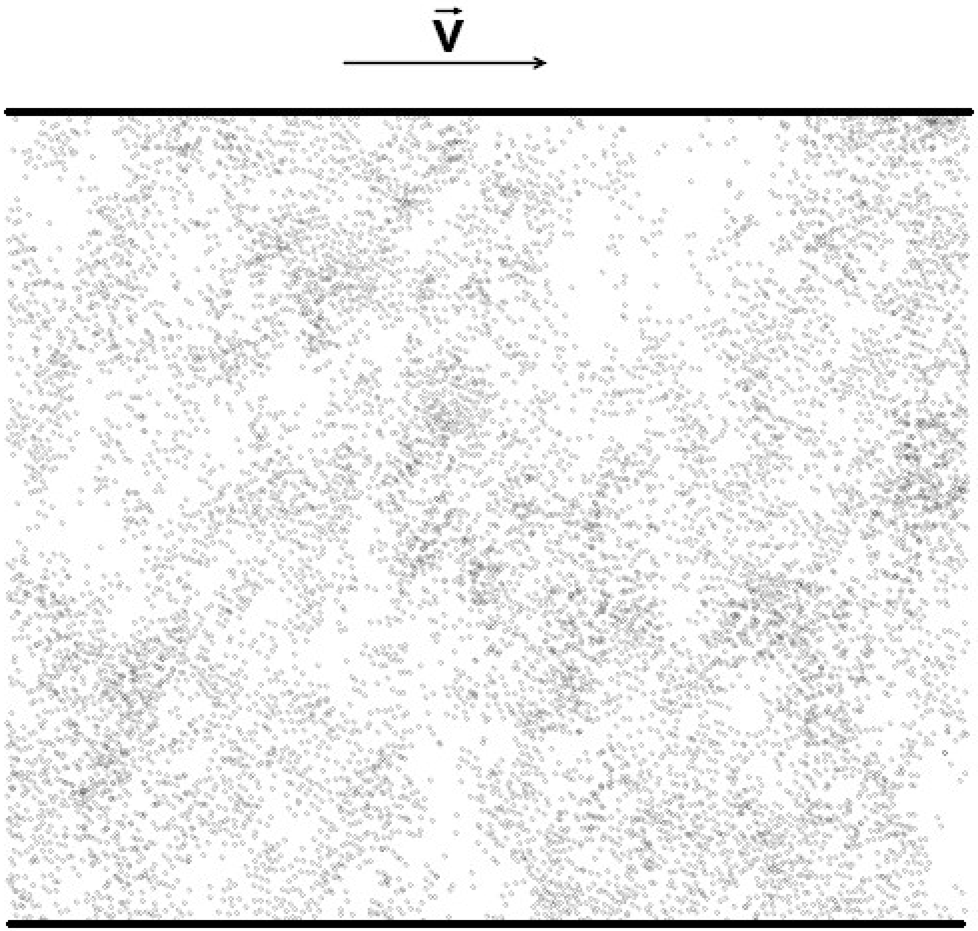
$$\langle |\delta p_{\perp \mathbf{q}}|^2 \rangle \sim 1/q^2$$

Continuity equation + wavelike modes -->

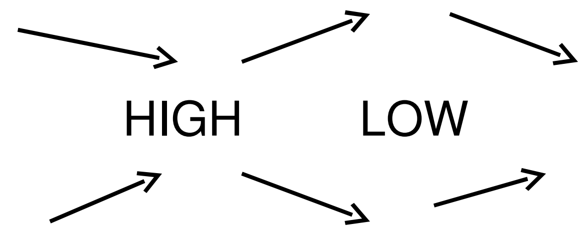
$$\delta c \sim \sqrt{c_0/P'(c_0)}\delta p_{\perp}$$

So variance of density fluctuations should also diverge!
Giant number fluctuations $\Delta N \sim N^a$, $a > ½$
Exponent values: dynamic RG Toner-Tu 1995, 1998

Flocks have big density fluctuations



Toner and Tu PRE 1998



Easy orientational
fluctuations lead to
large fluctuating mass flux

Polar active particles on surface cont'd

Simple consequence: interplay of "pressure"
and number conservation near onset of flocking:

$$\partial_t c = -\boldsymbol{\nabla} \cdot c\,\mathbf{p}$$

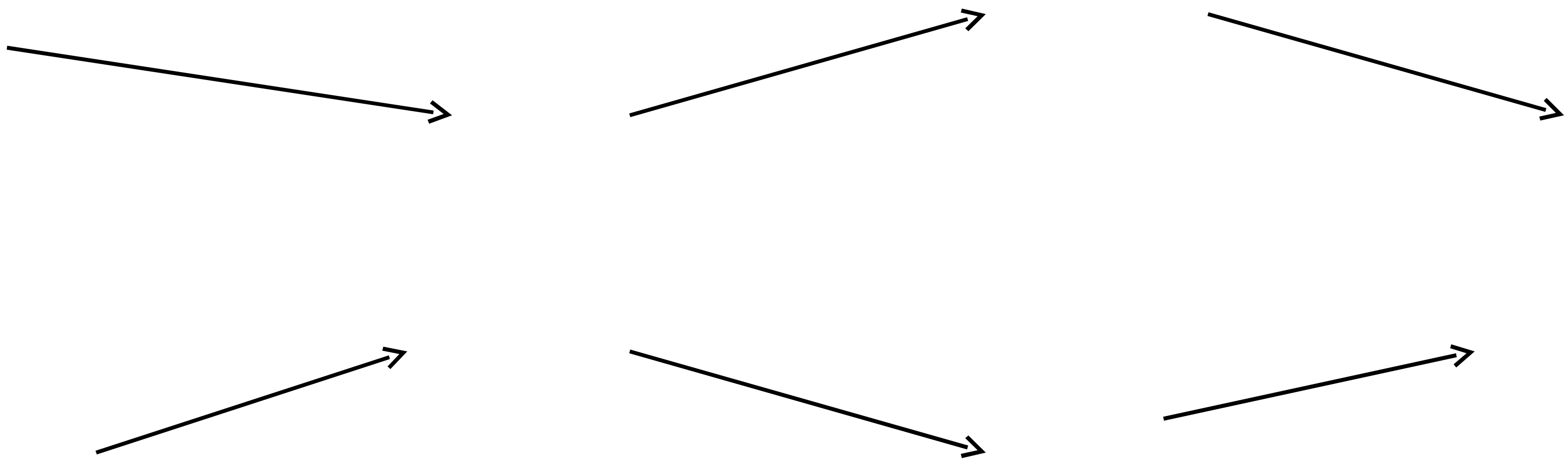
$$\partial_t \mathbf{p} + \lambda \mathbf{p} \cdot \nabla \mathbf{p} + \ldots = (\alpha - \beta \mathbf{p} \cdot \mathbf{p})\mathbf{p} + \Gamma \nabla \nabla \mathbf{p} - \nabla P(c) + \mathbf{f}$$

$\alpha \longrightarrow$ zero, approach flocking:
predict "sound" waves
(SR and Mazenko 1982) SR 2006; Baskaran/Marchetti 2007

Noise, α independent, no FDT:
density correlation length $\sim \alpha^{-1/2}$

SR 2006

Fluctuations suppress fluctuations! Long-range XY order in d=2



p is a velocity: δp reaches $\delta p\, t$ in time t: long-range interaction

p.grad p nonlinearity relevant, d<4

Dynamic RG Toner-Tu 1995, '98

Effective stiffness diverges at small q for d<4

Hence LRO in d=2

But effective only for d>1else no transverse fluctuations

Other issues in dry polar flocks

Order of transition: Chate et al vs Vicsek et al

Analytical theory: Mishra, Baskaran, Marchetti, SR

Instabilities and coherent structures in ordered phase

Real experiments: Giardina et al – starlings see topological nbhd

Locusts: Couzin and group

Bausch et al. Nature, to appear: actomyosin extracts

Apolar active system; slow variables

Apolar ordering: no macroscopic velocity

On substrate: ignore momentum conservation

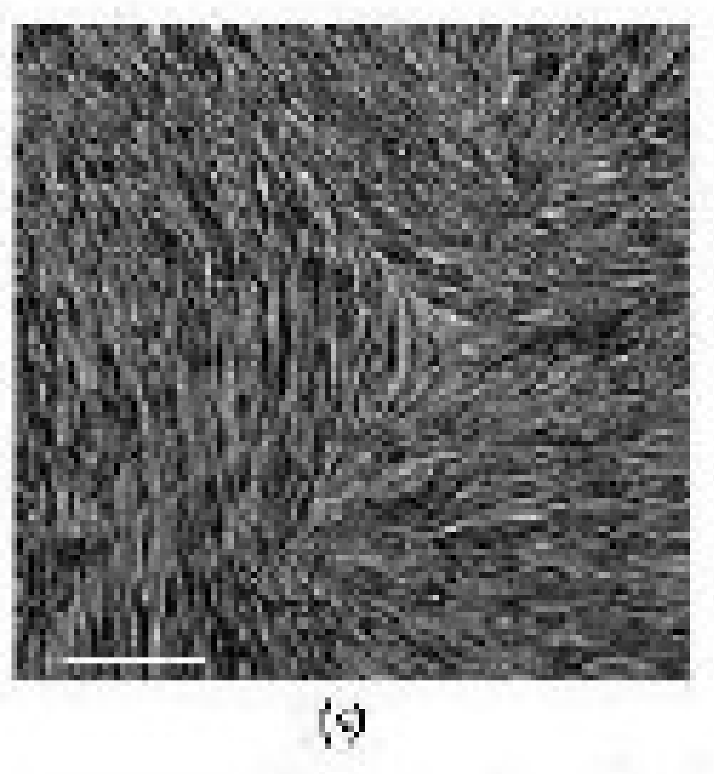
Slow variables: concentration $c(x,t)$

traceless symmetric order parameter Q_{ij}

SR, Simha, Toner EPL 2003

Building the equations of motion →

Living apolar order



Melanocyte nematics
Kemkemer et al. EPJE 1999

Strength -1/2 disclination:
living proof that order parameter
is unchanged under π rotation

Dry active nematic dynamics

Director field: standard

$$\partial_t \delta \mathbf{n}_\perp = \lambda_+ \partial_z \mathbf{v}_\perp + \lambda_- \boldsymbol{\nabla}_\perp v_z$$

flow-orientation coupling

$$+ K_1 \boldsymbol{\nabla}_\perp (\boldsymbol{\nabla}_\perp \cdot \delta \mathbf{n}_\perp) + K_2 \nabla_\perp^2 \delta \mathbf{n}_\perp + K_3 \delta_z^2 \delta \mathbf{n}_\perp$$

elasticity

$$+ \mathbf{f}_\perp$$

noise

Dry active nematic dynamics

concentration field: novel

$$\frac{\partial c}{\partial t} = -\nabla \cdot \mathbf{j}$$

Number conservation

$$m\frac{\partial \mathbf{j}}{\partial t} = -\Gamma \mathbf{v} - \nabla \cdot \sigma + \mathbf{f}_R$$

inter-action with substrate

inter-particle interaction

noise

Equations of motion for active nematic

$$\frac{\partial c}{\partial t} = -\nabla \cdot \mathbf{j}$$

Number conservation

$$m\frac{\partial \mathbf{j}}{\partial t} = -\Gamma \mathbf{v} - \nabla \cdot \sigma + \mathbf{f}_R$$

$$= -\Gamma\ \mathbf{v} - w_o \nabla c - w_1 \nabla \cdot (\mathbf{Q}c) + \mathbf{f}_R$$

substrate friction — pressure — activity — noise

$$\mathbf{Q} = [\mathbf{n}\mathbf{n} - (1/d)\mathbf{I}]S$$

$$\hat{\mathbf{n}} = (\cos\theta, \sin\theta)$$

$$\mathbf{n}(\mathbf{r}, \mathbf{t}) = \hat{\mathbf{z}} + \delta\mathbf{n}(\mathbf{r}, \mathbf{t})$$

$$\mathbf{j} = (j_x, j_z) \propto (\partial\theta/\partial z, \partial\theta/\partial x)$$

Equations of motion for active nematic

$$\frac{\partial c}{\partial t} = -\nabla \cdot \mathbf{j}$$

Number conservation

$\partial_t \boldsymbol{v} \ll \Gamma \boldsymbol{v}$ Velocity slaved to slow degrees of freedom

$$\boldsymbol{v} = -\alpha\Big(\partial_z \delta \boldsymbol{n}_\perp + (\nabla_\perp \cdot \delta \boldsymbol{n}_\perp)\hat{\boldsymbol{z}}\Big) - \gamma_1 \boldsymbol{\nabla}_\perp c - \gamma_2 \partial_z c \hat{\boldsymbol{z}} + \frac{\boldsymbol{f}_{\mathrm{R}}}{\Gamma}$$

Effective eqs of motion for concentration, director:

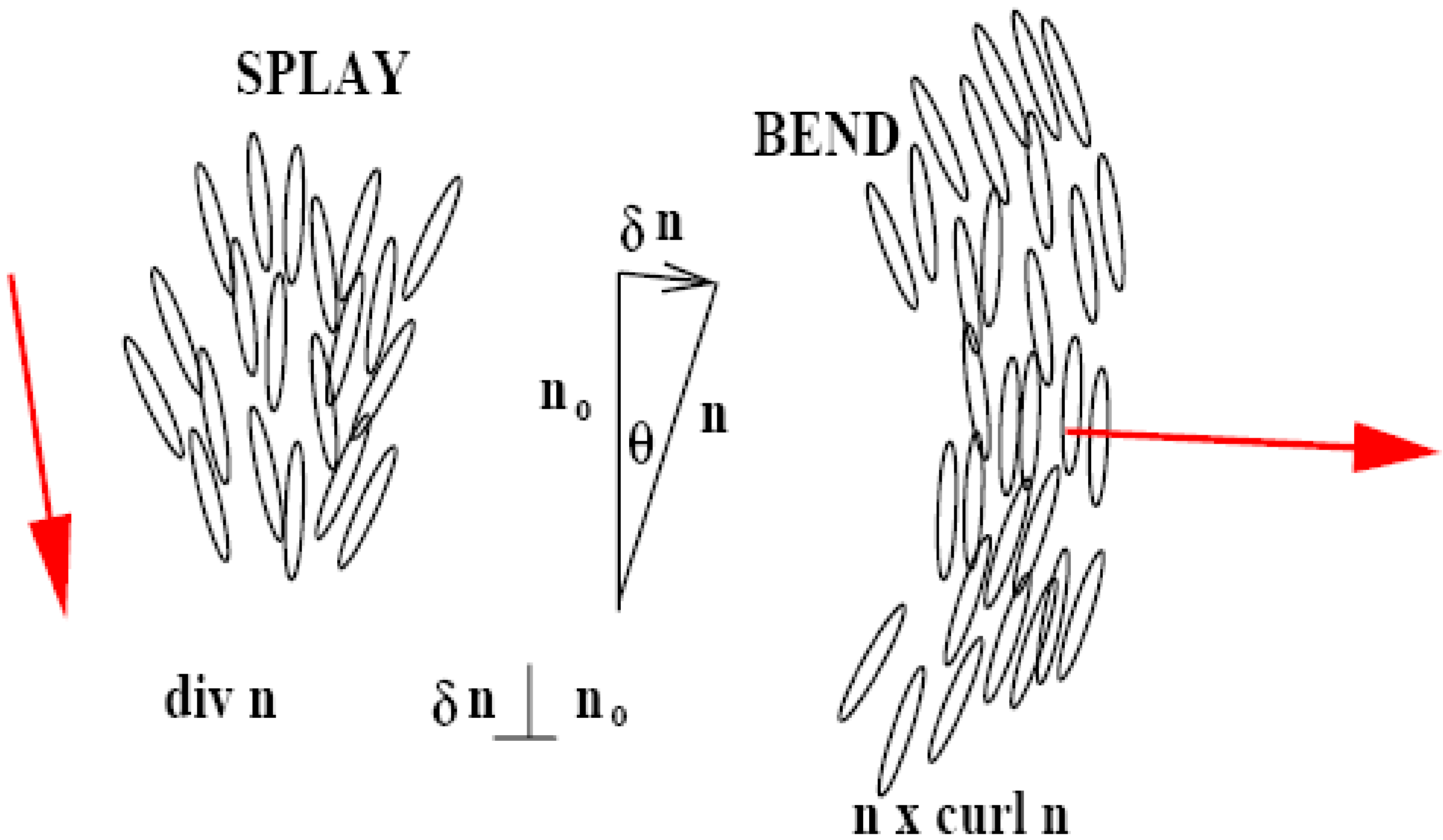
Coupled dynamics: concentration and orientation

$$\frac{\partial \delta c}{\partial t} = \left(D_z \partial_z^2 + D_\perp \nabla_\perp^2\right)\delta c + 2c_0 \alpha \partial_z (\nabla_\perp \cdot \boldsymbol{\delta n}_\perp) + \nabla \cdot \boldsymbol{f}_c$$

$$\frac{\partial \boldsymbol{\delta n}_\perp}{\partial t} = \left(K_z \partial_z^2 + K_\perp \nabla_\perp^2 + K'_{\mathrm{L}} \boldsymbol{\nabla}_\perp \boldsymbol{\nabla}_\perp\right) \cdot \boldsymbol{\delta n}_\perp + D_{cn} \partial_z \boldsymbol{\nabla}_\perp \delta c + \boldsymbol{f}_\perp$$

$$\langle \delta c(\boldsymbol{q}, t) \delta c(-\boldsymbol{q}, t) \rangle = \int_{-\infty}^{\infty} \frac{\mathrm{d}\omega}{2\pi} \langle |\delta c(\boldsymbol{q}, \omega)|^2 \rangle = \frac{(2c_0 \alpha q_\perp q_z)^2 \Delta_n}{F(\hat{\boldsymbol{q}}) q^6} \propto \frac{1}{q^2}$$

$$F(\hat{\boldsymbol{q}}) \equiv 2\big(D_c(\hat{\boldsymbol{q}}) + K_{\mathrm{L}}(\hat{\boldsymbol{q}})\big)\big[D_c(\hat{\boldsymbol{q}}) K_{\mathrm{L}}(\hat{\boldsymbol{q}}) - 2c_0 \alpha D_{cn} \hat{q}_\perp^2 \hat{q}_z^2\big].$$



ASYMMETRY LEADS TO CURRENT

$$J_x \propto \partial_z \theta \qquad J_z \propto \partial_x \theta$$

Calculating number fluctuations

Langevin equations for concentration c and angle θ fields →

At wavevector q: $\langle|\theta_q|^2\rangle \sim 1/q^2$

as in thermal equilibrium

Diffusive current J ~ grad c

Active current $J_x \propto \partial_z \theta$ $J_z \propto \partial_x \theta$

Concentration, angle fluctuations similar

Giant number fluctuations

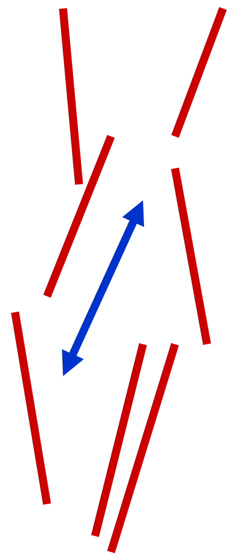
Thus $<|\delta\ c_q|^2> \sim 1/q^2$

i.e.

$<(\delta\ N)^2>/N \sim N^{2/d}$ Dimension d

$\delta\ N \sim N$ d=2

First confirmation: computer experiments



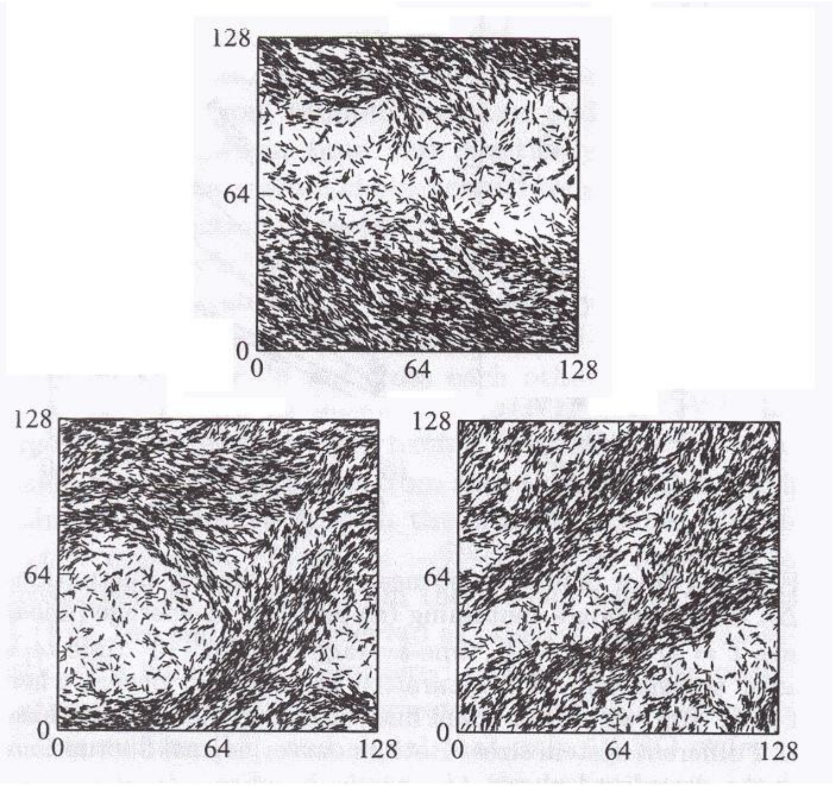
Chaté et al., PRL **96**, 180602 (2006)

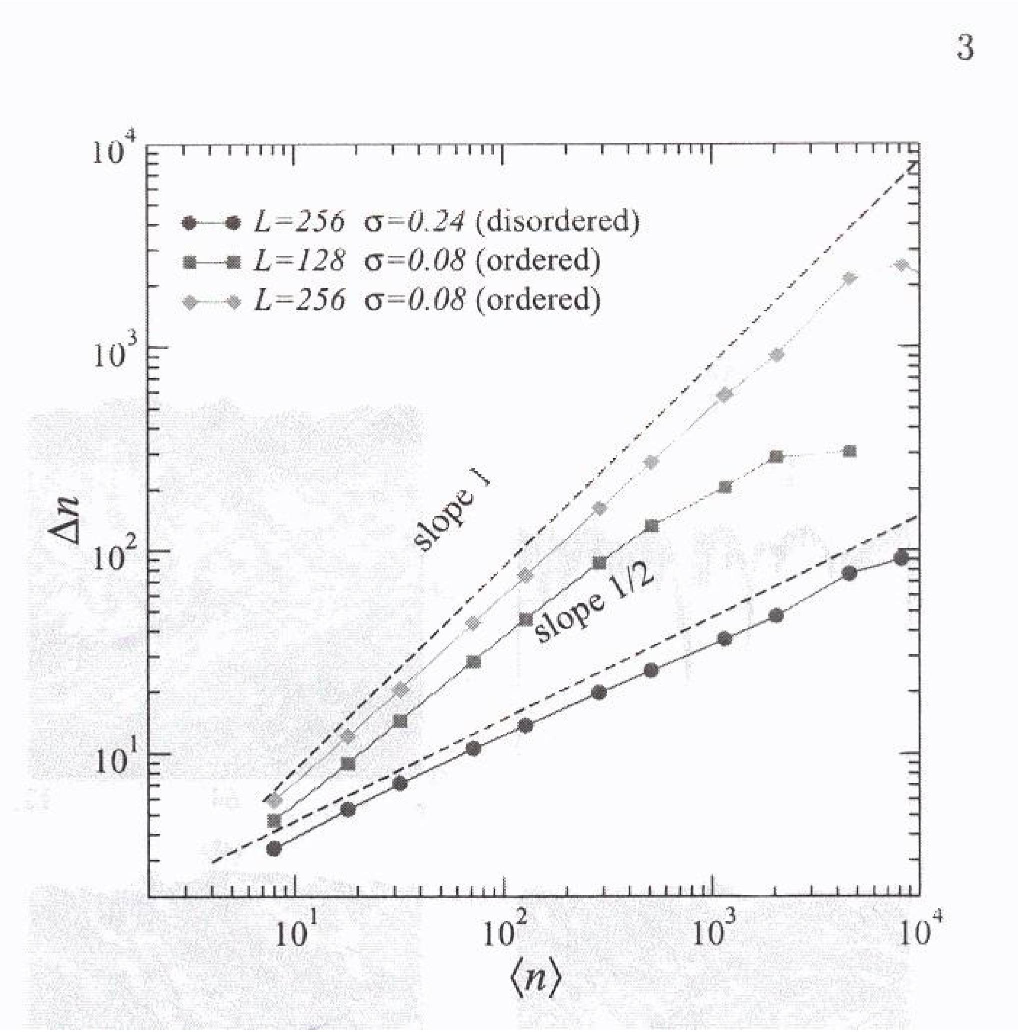
Align with mean of neighbours
+ small angular noise

Fixed small step forward or back along length

Parameters: angular noise, number density

First confirmation: computer experiments



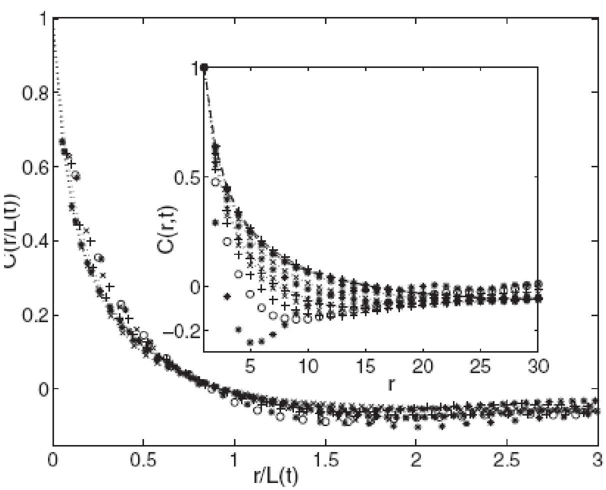


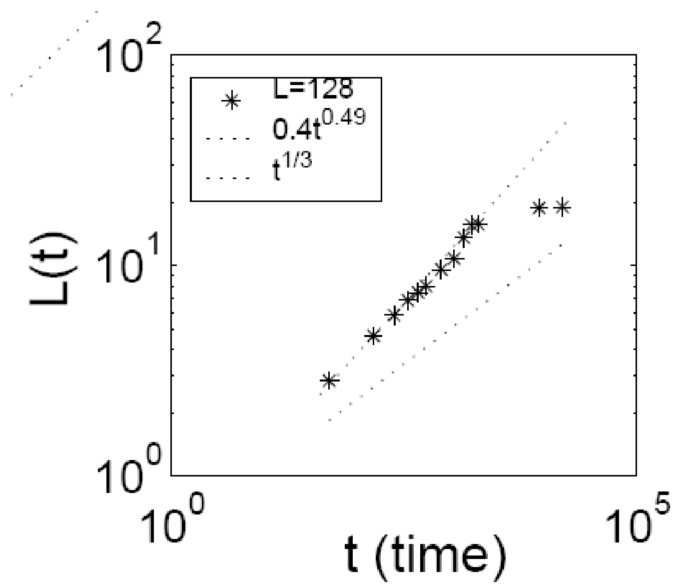
Chaté et al., PRL **96**, 180602 (2006)

Active nematics are intrinsically phase-separated

Mishra+SR PRL 2006: passive particles driven actively by fluctuations of an ordered active nematic

– intrinsically phase separated, density *clusters* as $t^{1/2}$ (not 1/3)





Pair correlator has cusp:
no Porod's law, poor interfaces

cf. Das-Barma PRL 85 1602(2000)

Approach to ordered phase

Quench from isotropic, uniform-density state: how do nematic order and density fluctuations grow?

Microscopic and coarse-grained approaches

Start with Chaté *et al.* flocking rule
Microscopic definitions of
nematic order parameter Q, density ρ
Build coarse-grained PDEs with noise
Do they look like SR-Simha-Toner?
Is noise important?

Shradha Mishra PhD thesis 2009; Mishra et al. 2010

Deriving continuum equations of motion

Mishra, Ginelli, Chaté, Puri, SR 2008-10

$$\frac{\partial \rho}{\partial t} = a_2\, \partial_\alpha \partial_\beta \left(\rho\, [\mathbf{Q}]_{\alpha\beta}\right) + \frac{a_2}{2} \nabla^2 \rho + a_1 \nabla \cdot \sqrt{\rho}\, \mathbf{n} \eta$$

$$\text{anisotropic diffusion term } T_m \equiv a_2 \partial_\alpha \left([\mathbf{Q}]_{\alpha\beta} \partial_\beta \rho\right)$$

$$\text{non-equilibrium term} \quad T_c \equiv a_2 \partial_\alpha \left(\rho \partial_\beta [\mathbf{Q}]_{\alpha\beta}\right)$$

$\mathbf{n}$ = local principal axis of $\mathbf{Q}$

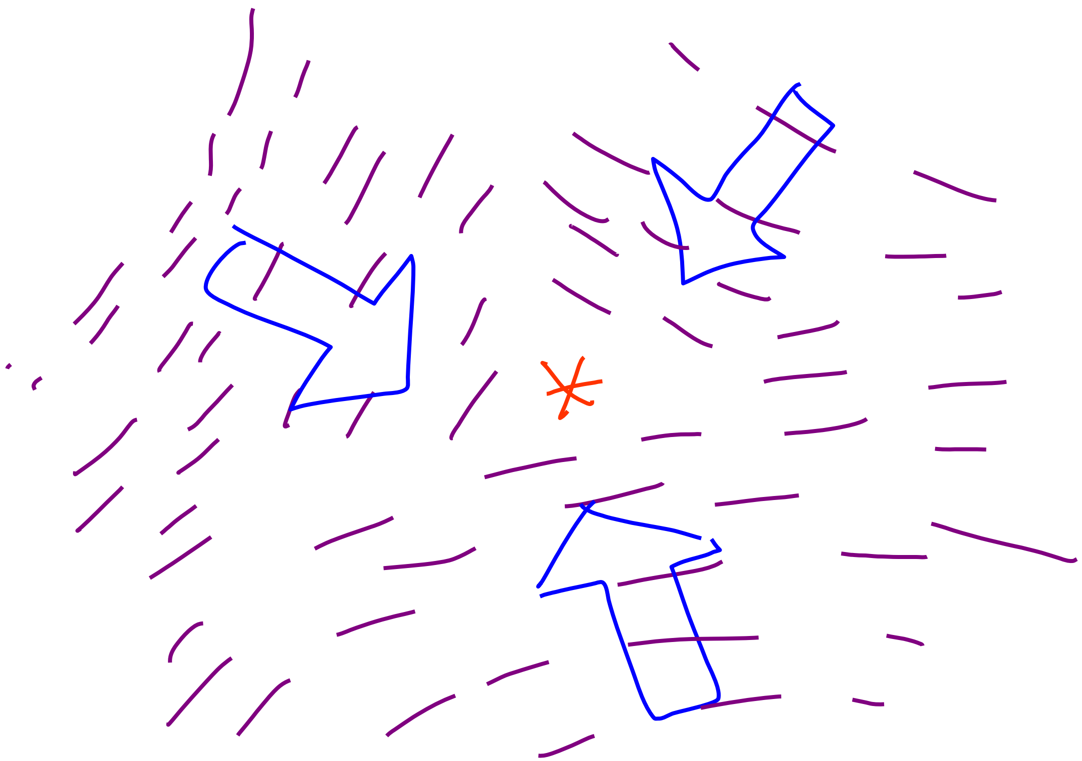
Numerical studies: continuum and particle models

- Approach to ordered phase, with and without noise
- Ordered phase: giant fluctuations, time-correlations
- Role of multiplicative noise
- Random *vs* ordered initial conditions

Mishra, Ginelli, Chaté, Puri, SR
2008

Kinetics of domain growth

Start with isotropic state, uniform density:
Defect motion causes clumping as nematic orders

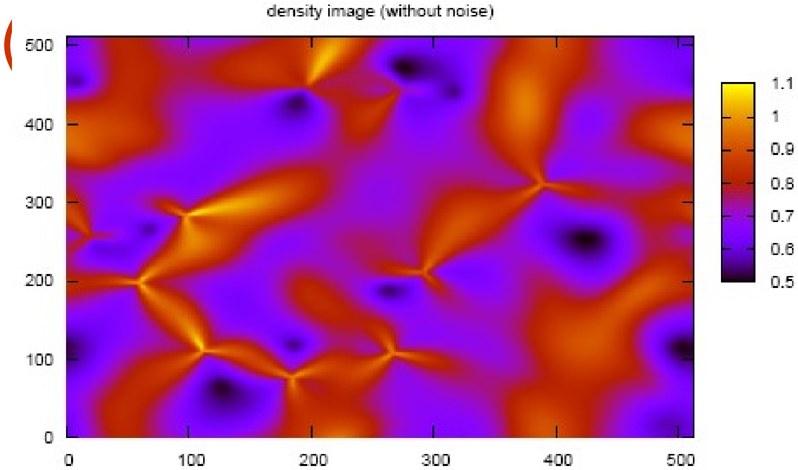


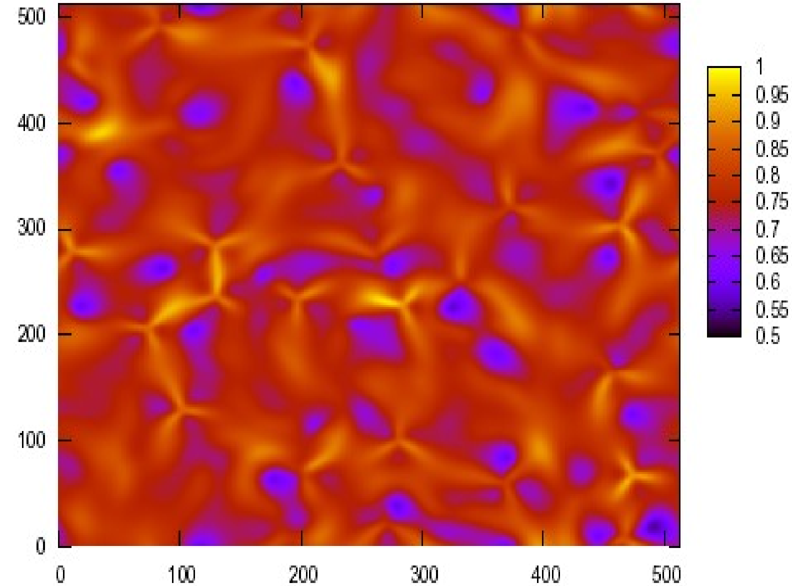
Curvature → mass flux

Shradha Mishra *et al* 2008

Coarsening

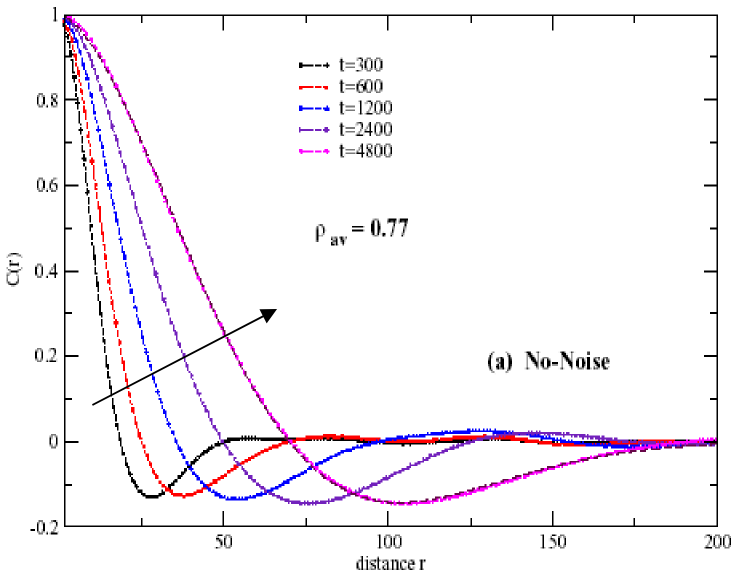
3-armed density bands around -1/2 defects





Dynamics: defect annihilation

Nematic order *and* density coarsen as $t^{1/2}$



More details including effect of noise: Mishra et al. 2008

DEAD ACTIVE PARTICLES: EXPERIMENTS

- vibrated granular matter:

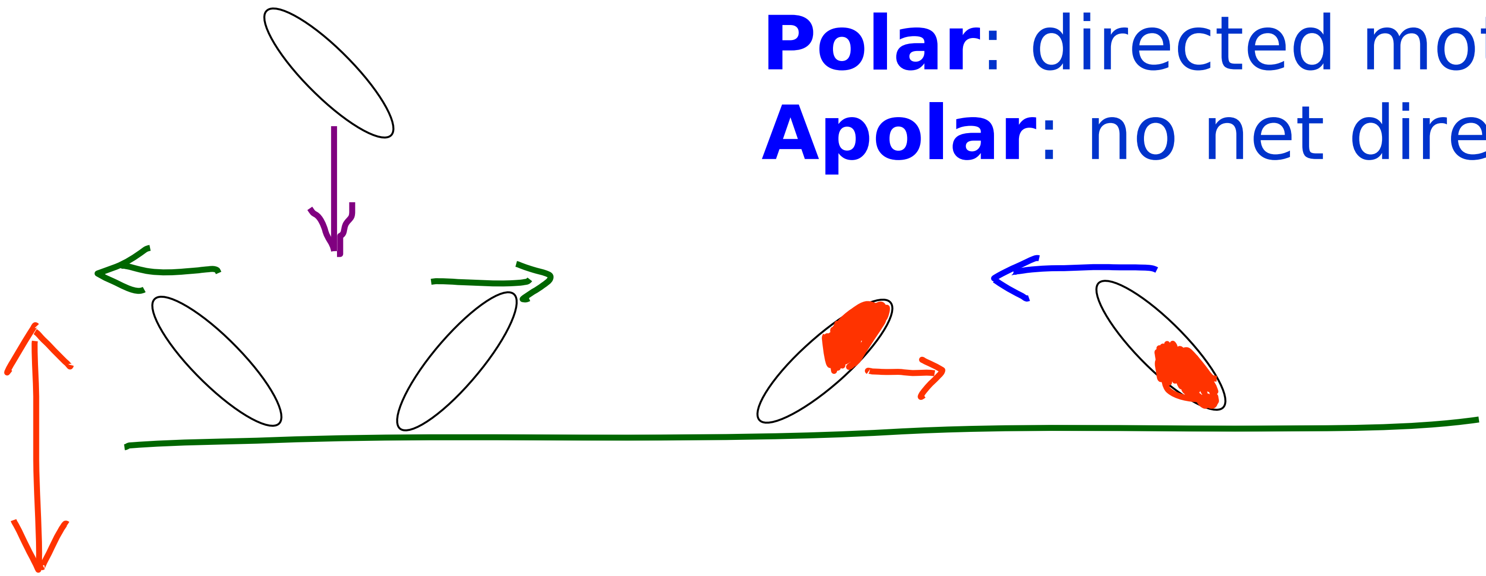
  a model active system

- experiments

Dead active particles

Tilt = motor coordinate
Shaking = energy input to each particle

Polar: directed motion
Apolar: no net direction



vibrate

Granular rods *are* self-driven!

Yamada et al., Kudrolli *et al.*, Aranson, Volfson

- Granular systems: testing ground for active-matter theories
- Real-space imaging
  - Count all particles, measure all orientations
- Access to space-time data
  - Measure time-series, correlators

V. Narayan (IISc)
N. Menon (UMass), SR: *Science* **317**, 105 (2007);
JSTAT 2006

Nematogens: Apolar and Polar

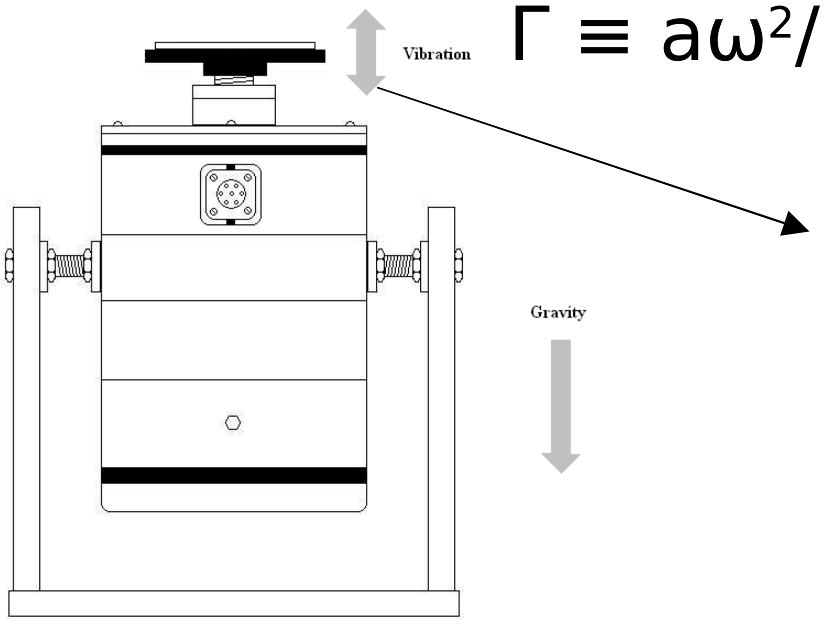
cylinders

bail
s

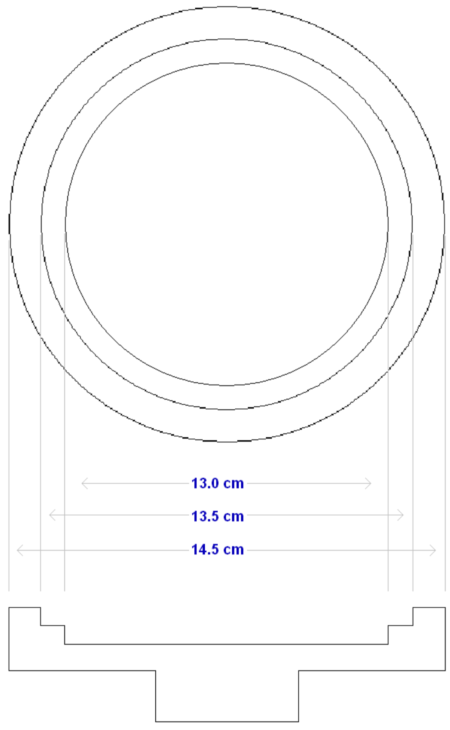
arrowhead
s

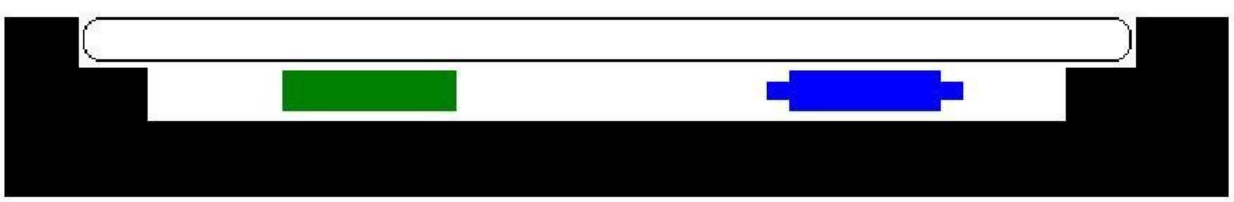
ROLLING PINS AND CYLINDERS

The Experiment



$\Gamma \equiv a\omega^2/g$

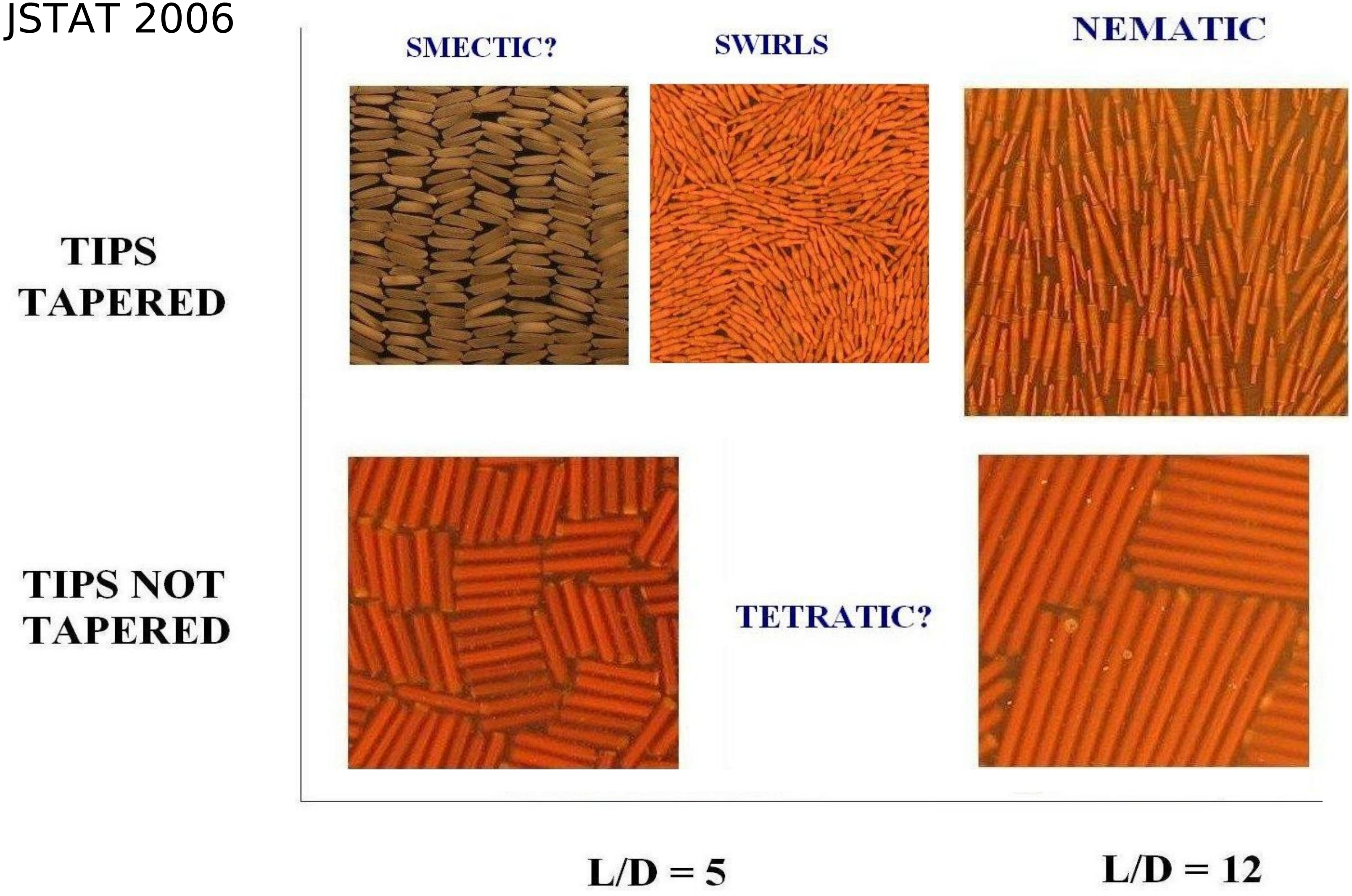




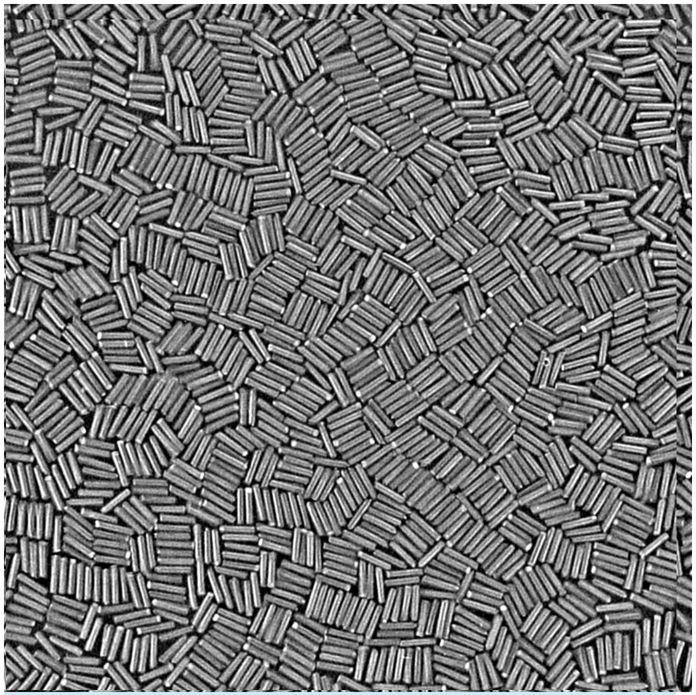
Equipment courtesy V. Kumaran and P.R Nott

“Phase” Behaviour

JSTAT 2006



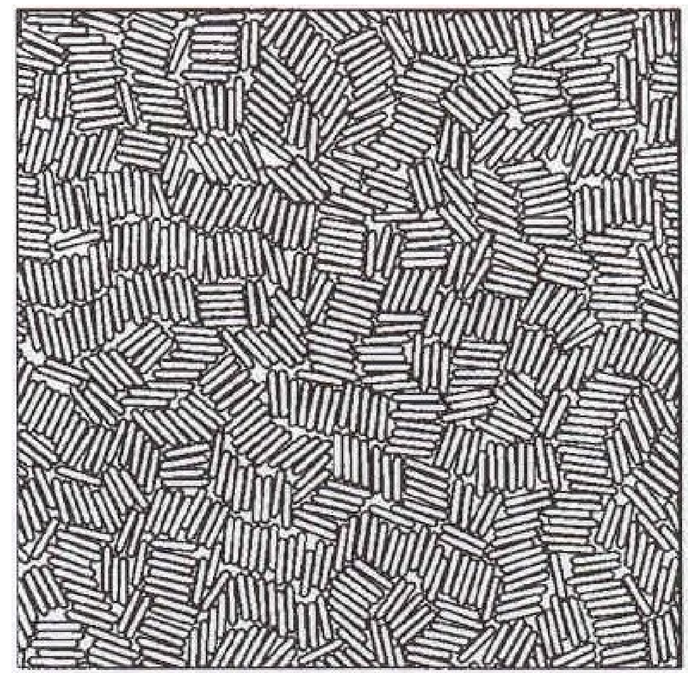
Tetratics: experiment vs simulation



EXPERIMENT

(AREA FRACTION = 80%)

Narayan et al JSTAT 2006



SIMULATION

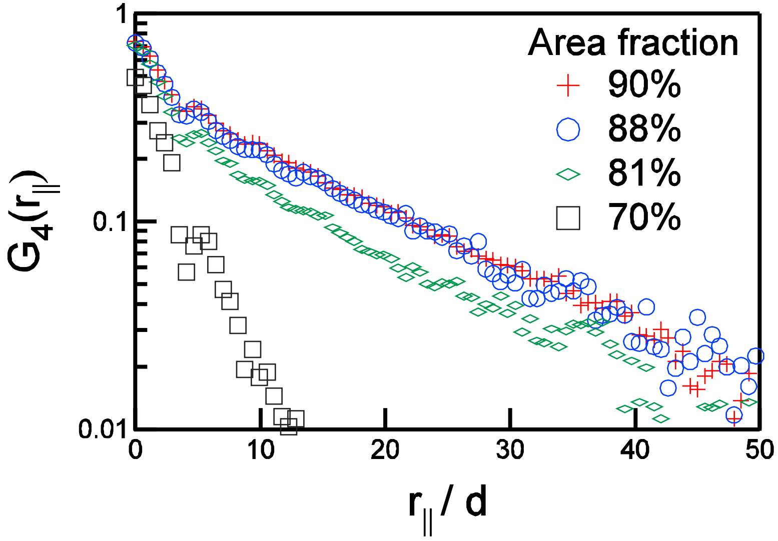
(AREA FRACTION = 75%)

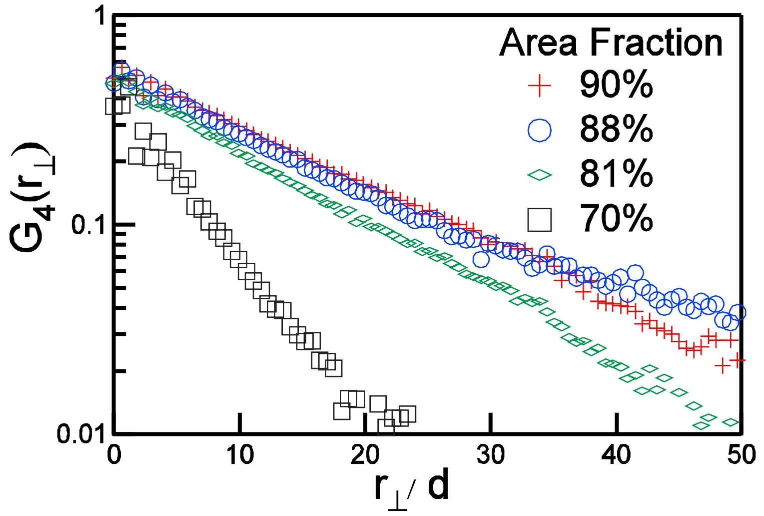
Bates and Frenkel JCP 2000

A Ghosh, D Dhar arXiv:cond-mat/0611361

Results : Tetratics

Short Cylinders





$$G_4(r) = \sum \cos[4\{\theta_i - \theta_j\}]$$

Narayan, Menon and Ramaswamy J. Stat. Mech. (P01005) 2006

A very active nematic

N = 2820

Γ = 5

Movie sped up 75x

Testing the theory

Vijay Narayan, SR and Narayanan Menon

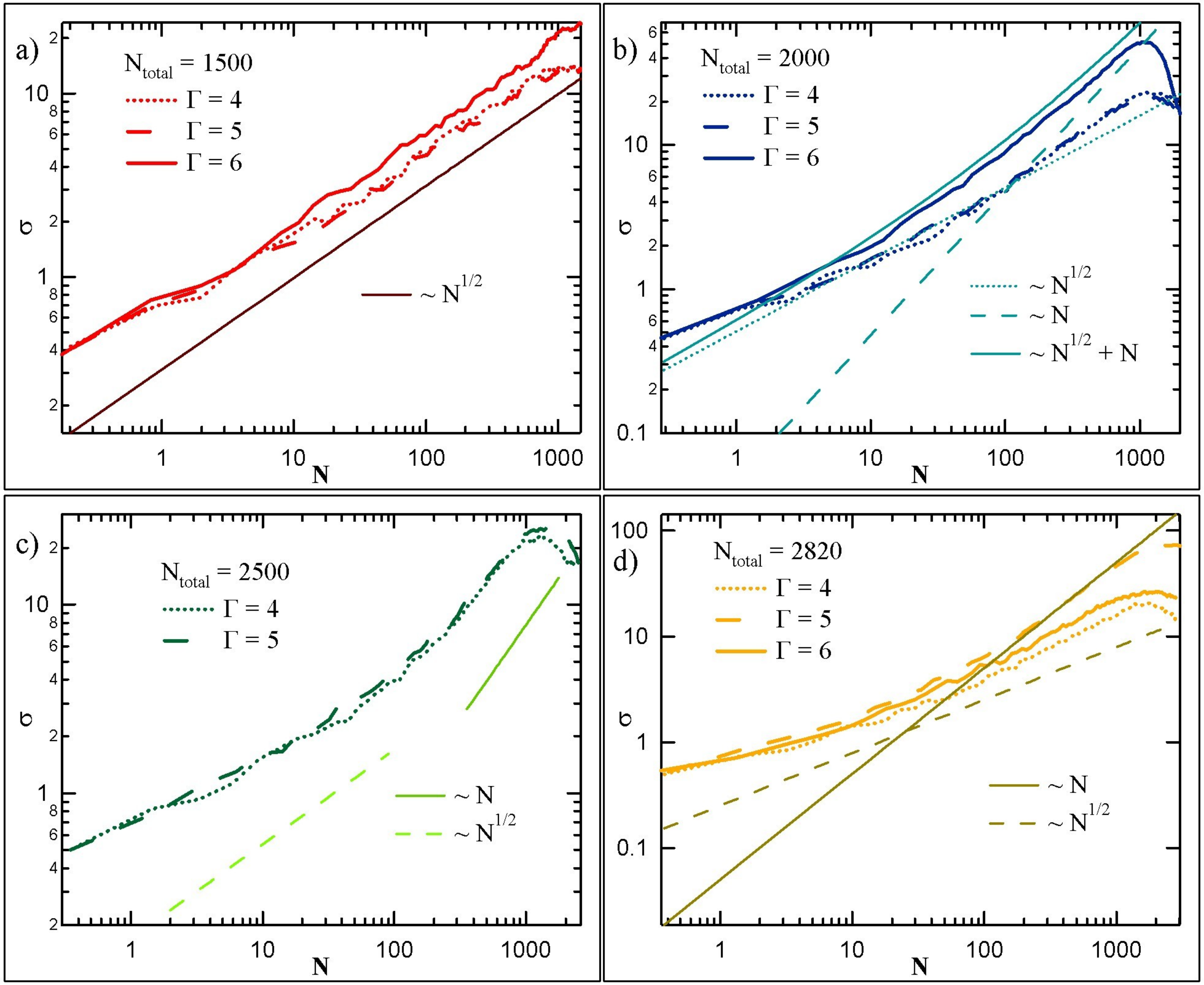
Science **317**, 105 (2007);

- Longitudinal sliding of particles (Chaté *et al.*.2006, Mishra *et al.* in prep.)
- Local curvatures induce currents (SR *et al.* 2003)
- Giant number fluctuations $\delta N \sim N$
- Logarithmic decay of local density autocorrelator

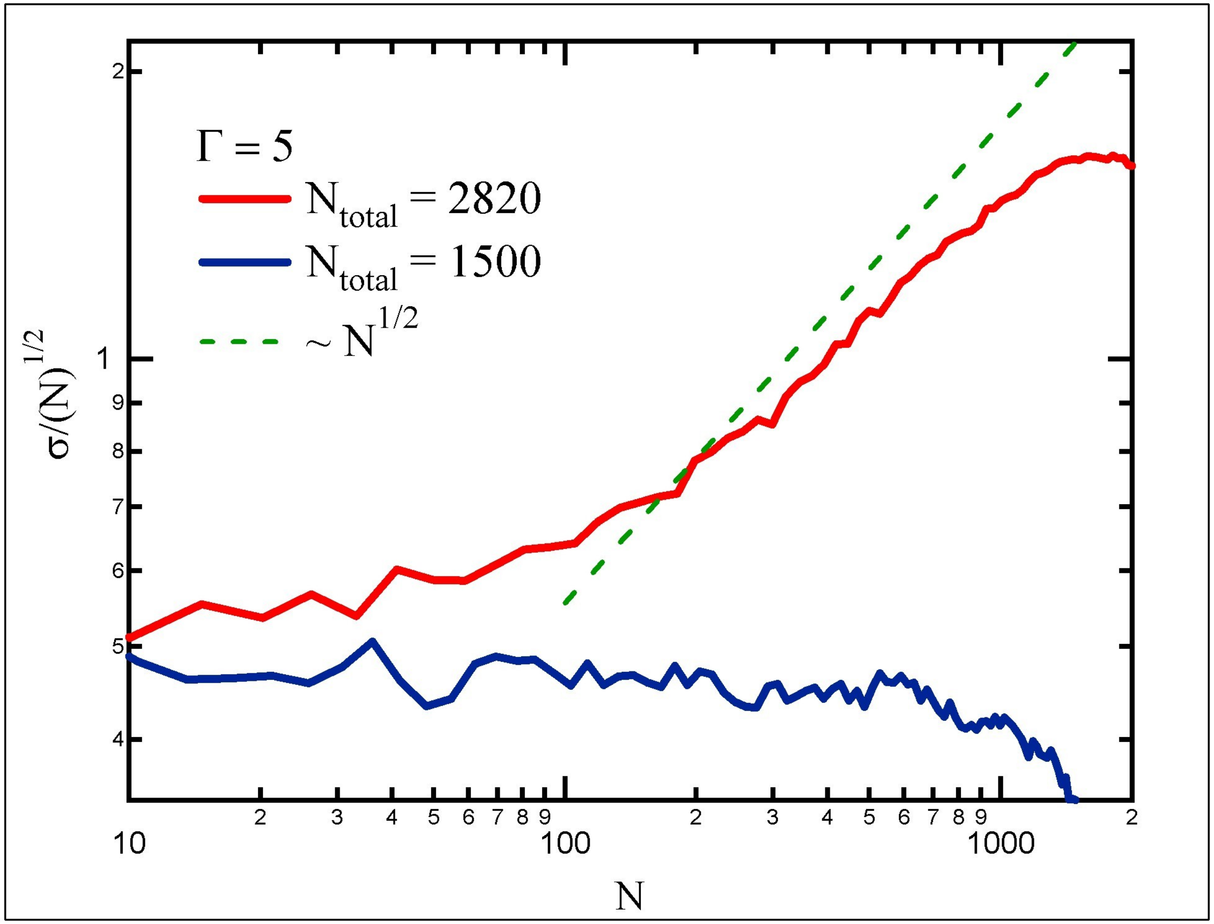
Standard Deviation vs Mean

- Take “windows” of different sizes in the sample plate
- Calculate mean number of particles in each window
- Calculate the fluctuations in the number of particles for each window
- Plot Standard Deviation vs Mean

Giant number fluctuations!



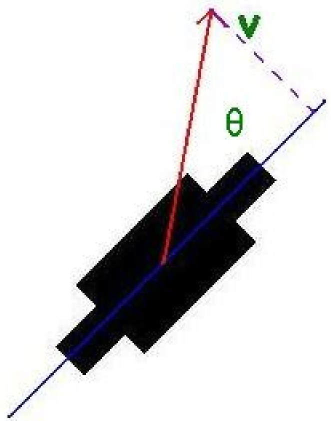
Fluctuation excess: $\Delta N/N^{1/2}$ *vs* N

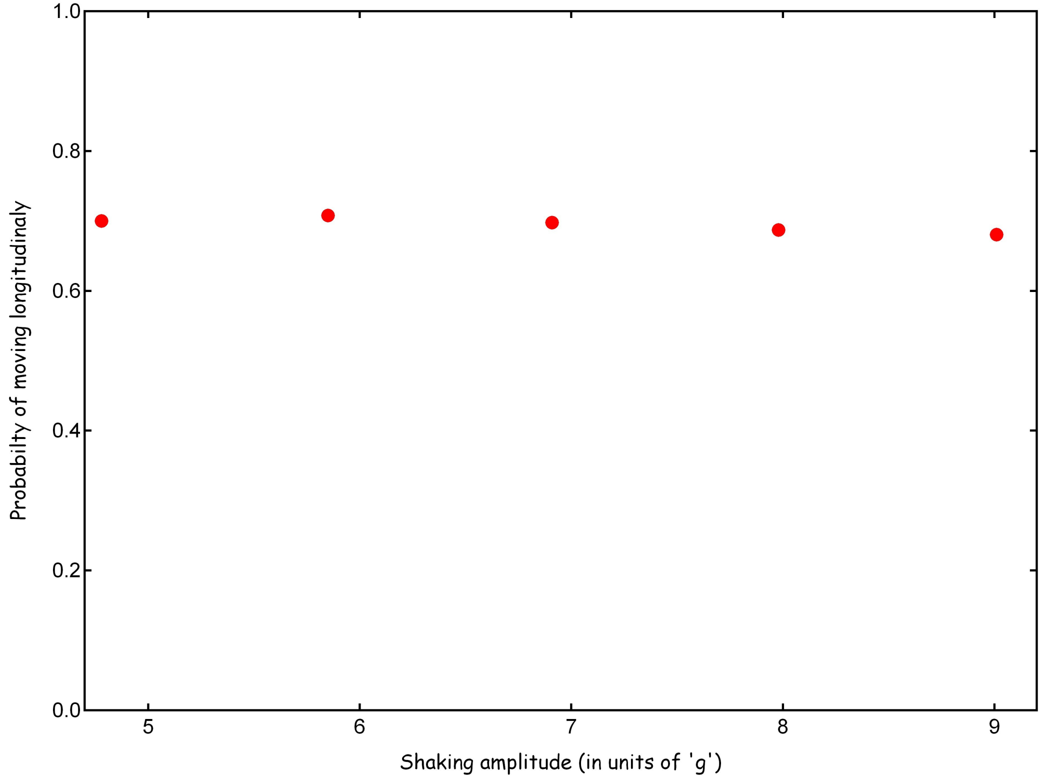


Science
317 (2007)
105

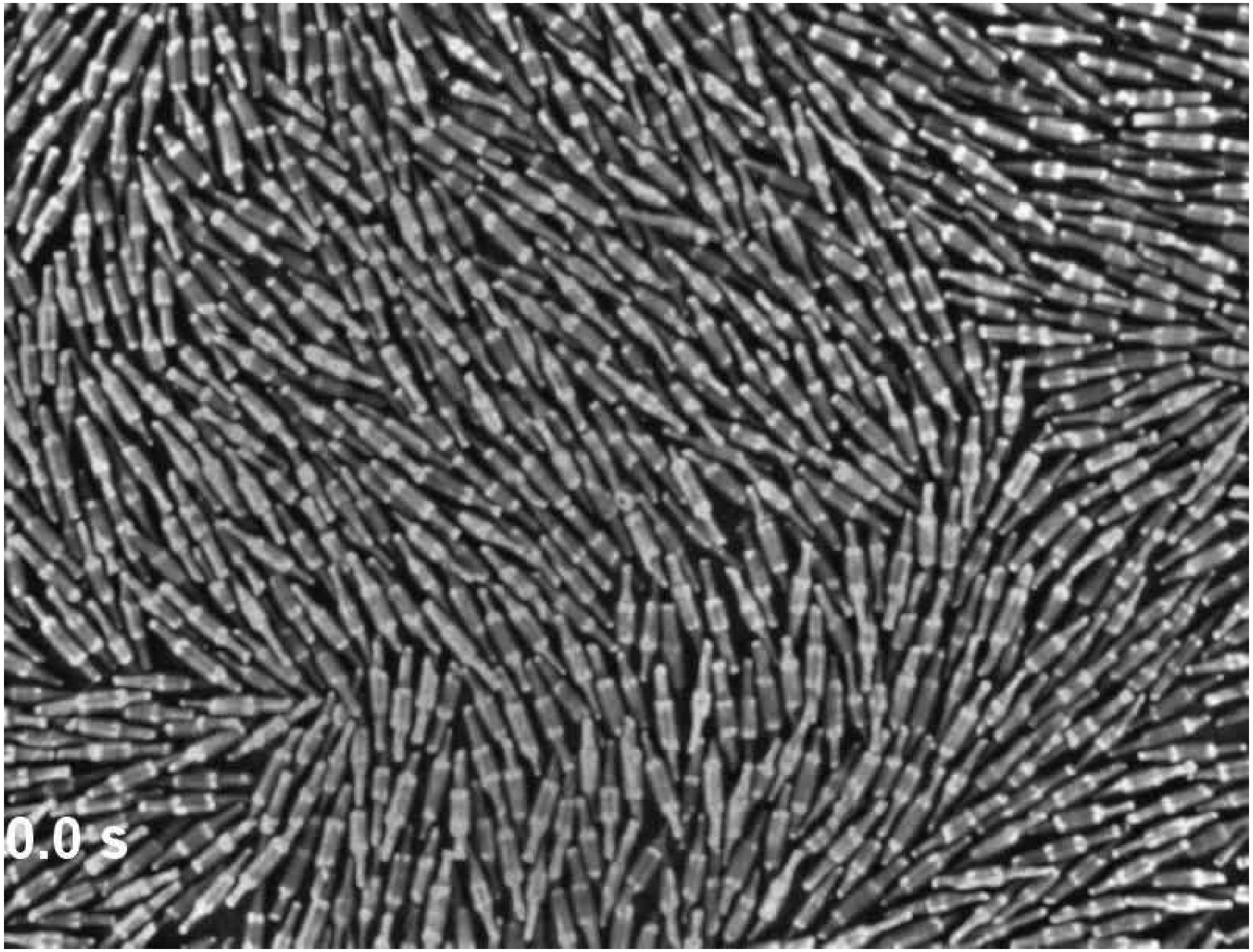
Anisotropic Displacement

2.2 times more likely to move along length

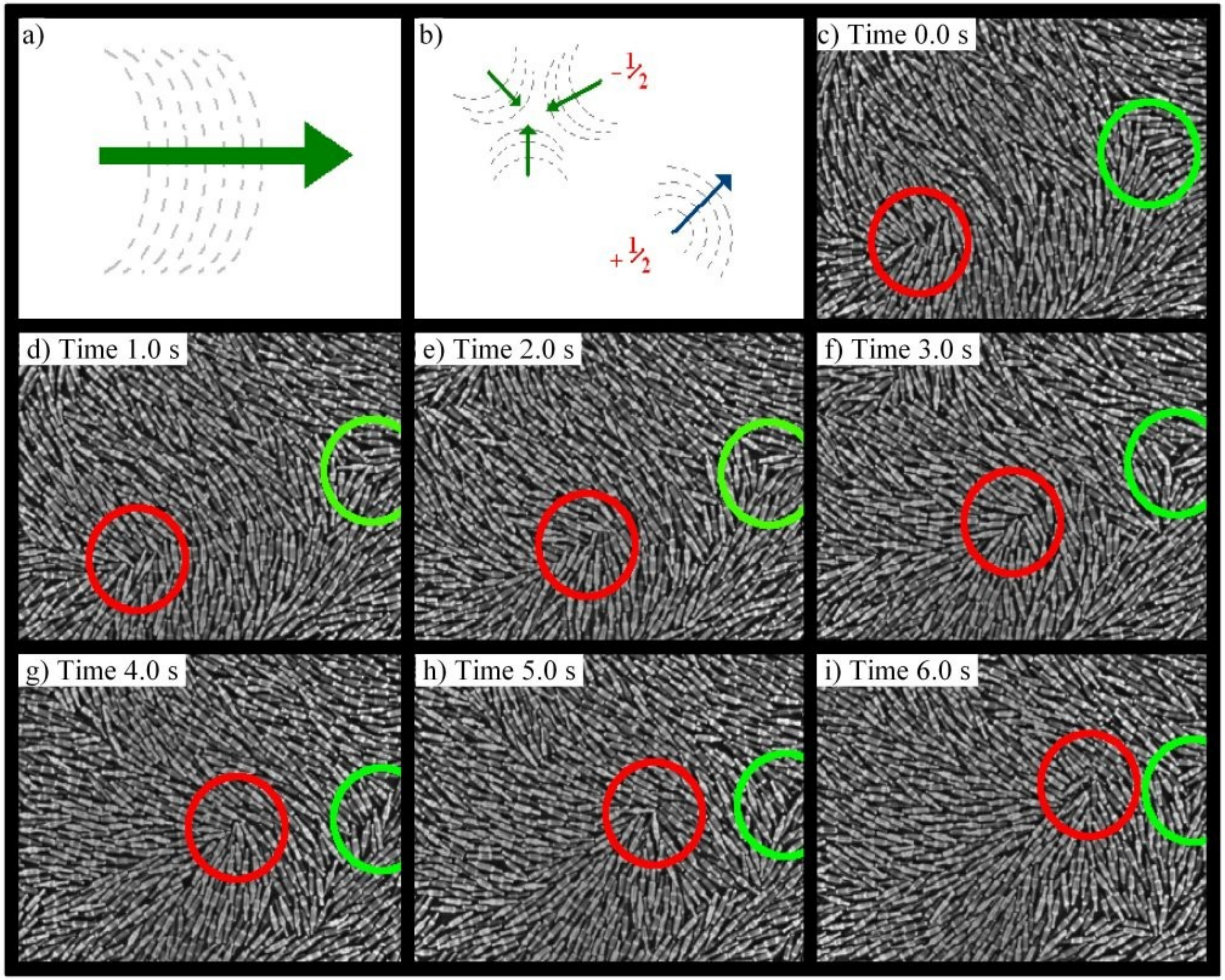




Currents from curvature around defects



Currents from curvature around defects



Local density time-correlator

Time correlations of density for an active nematic

$$S(q,t) \sim (1/q^2)\, \exp(-q^2 t)$$

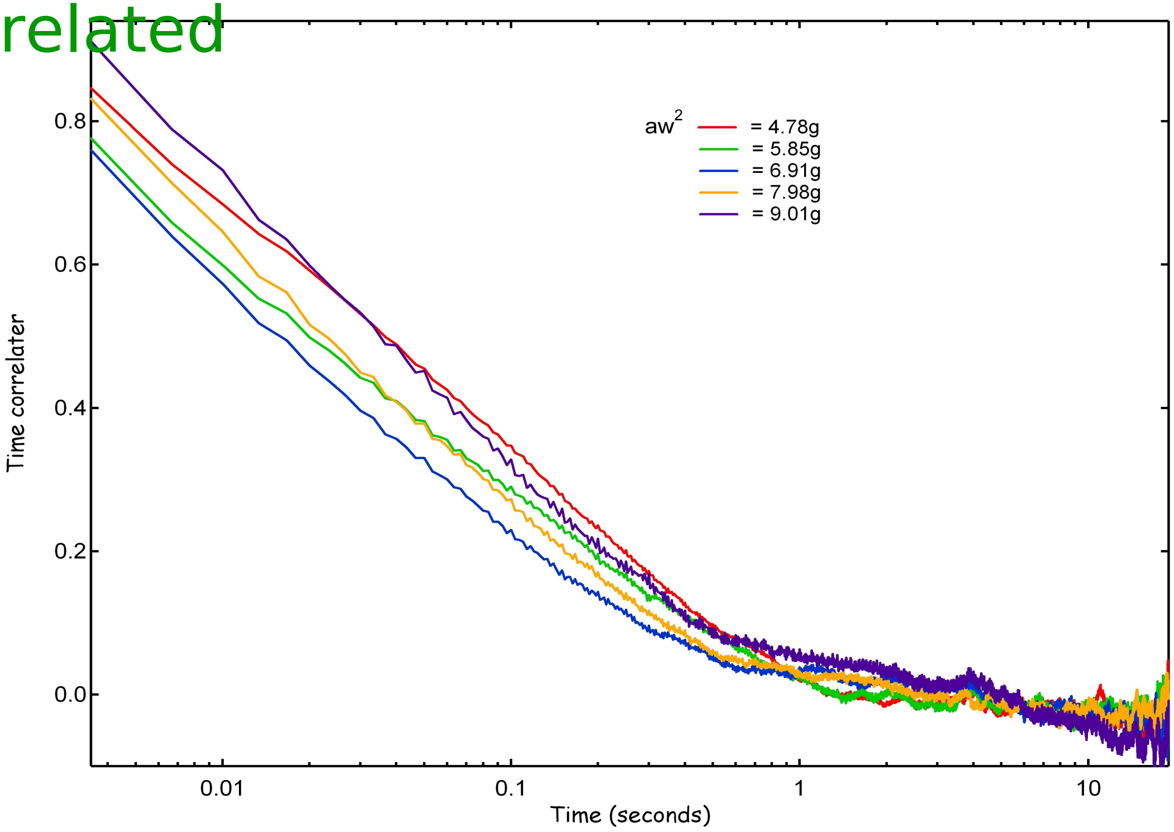
- $C(t) \equiv \langle \rho(\mathbf{x},0)\rho(\mathbf{x},t)\rangle = \int d\mathbf{q}\, S(\mathbf{q},t)$

$$\sim \log(1/t),\ t_{min} < t < t_{max}$$

- Contrast: $1/q^2$ prefactor absent for uncorrelated diffusors at thermal equilibrium, expect $1/t$

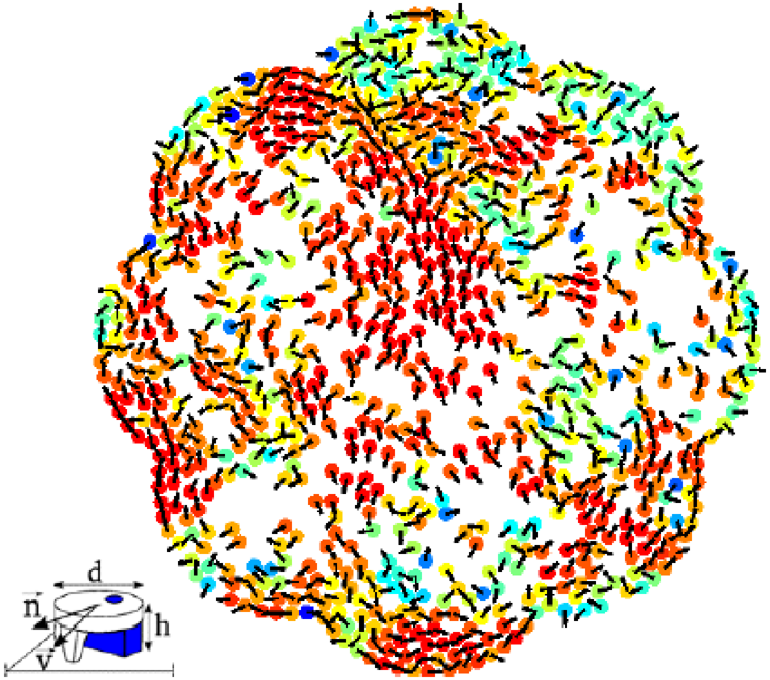
Local density time-correlator

Density at each coarse-grained point, autocorrelated



Log t

Polar granular flocks



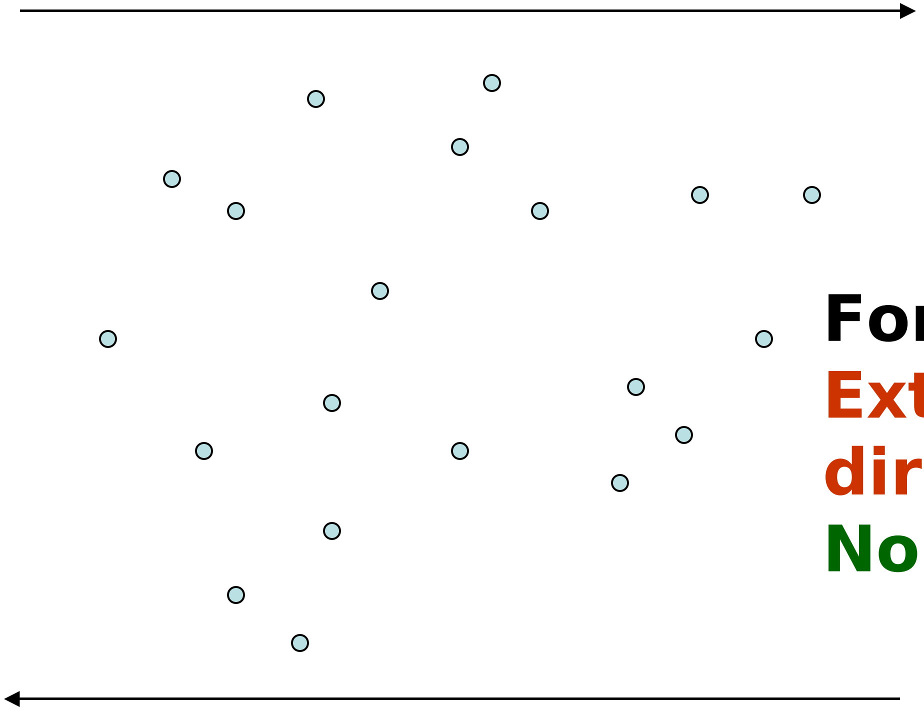
Deseigne et al 2010
Discs: shape and packing isotropic
Motion polar
See flocking, number fluctuations
Exponent consistent with Toner-Tu

ACTIVE PARTICLES IN A FLUID

- earlier work
- active thin fluid films
- chiral suspensions

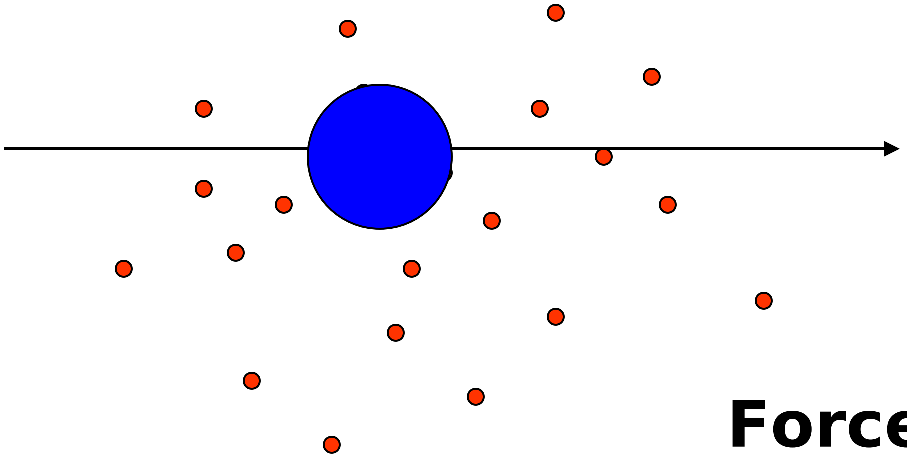
Contrast with other driven suspensions

Shear: drive from boundary



Force-free
Externally directed
No drift

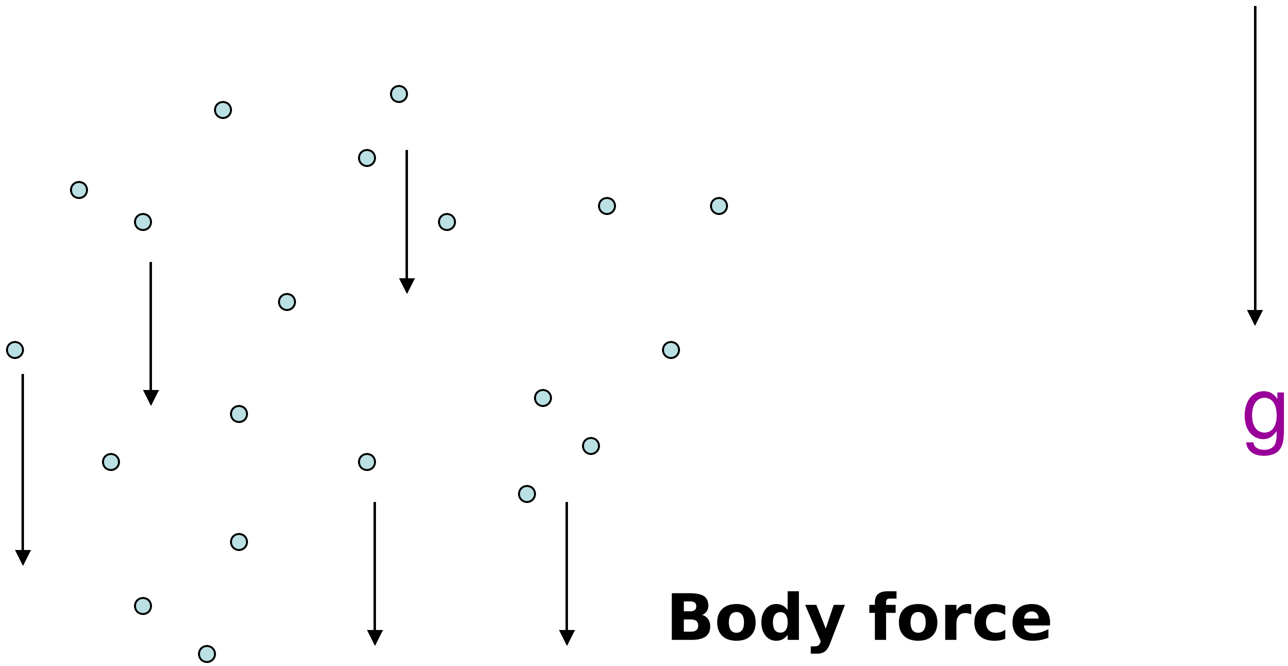
Electrophoresis: driven in bulk



Force (co-ion + counterions) =0

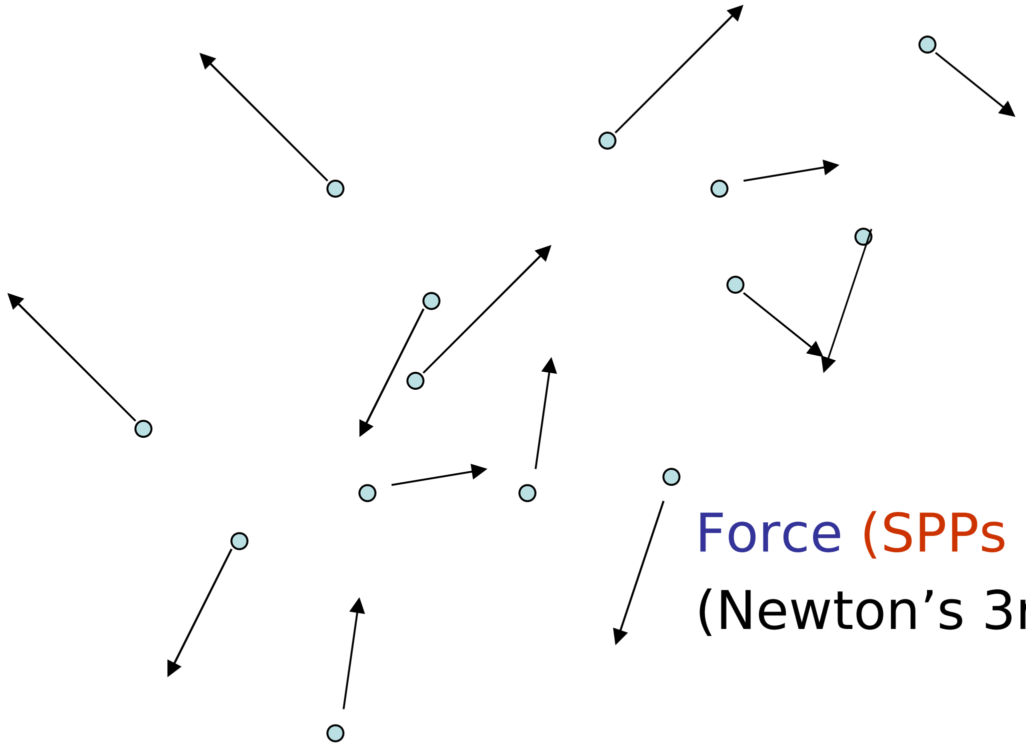
Force-free
Externally directed
Nonzero drift

Sedimentation: driven in bulk



Body force
Externally directed
Nonzero drift

Self-propulsion: driven in bulk

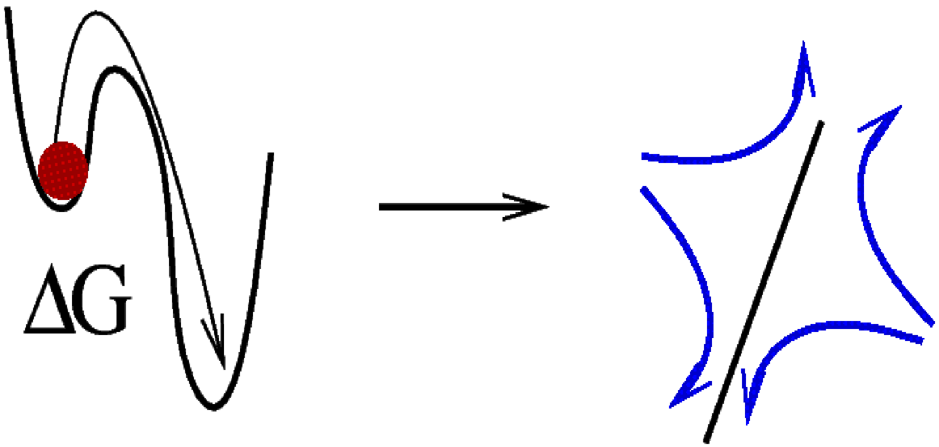


But force-free
Internally directed
Mean drift depends on state of order

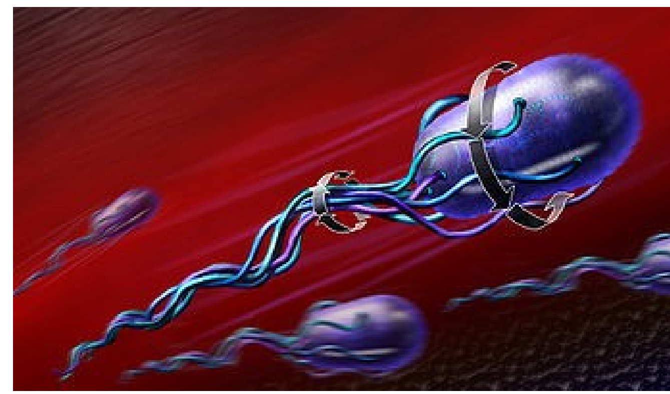
Force (SPPs + medium) =0
(Newton's 3rd Law)

Contrast with sedimentation, electrophoresis, shear

Minimal active particle = force dipole



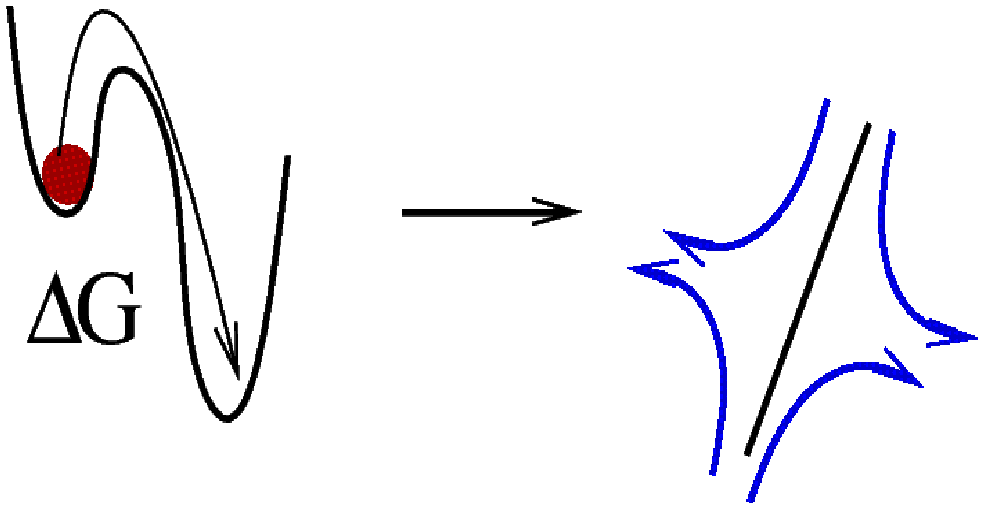
Extensile active particle
PUSHER



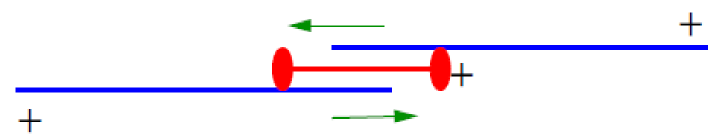
http://en.wikipedia.org/wiki/Escherichia_coli

- Active particles consume free-energy
- Move and stir surrounding medium
- Require no *external* force

Minimal active particle = force dipole



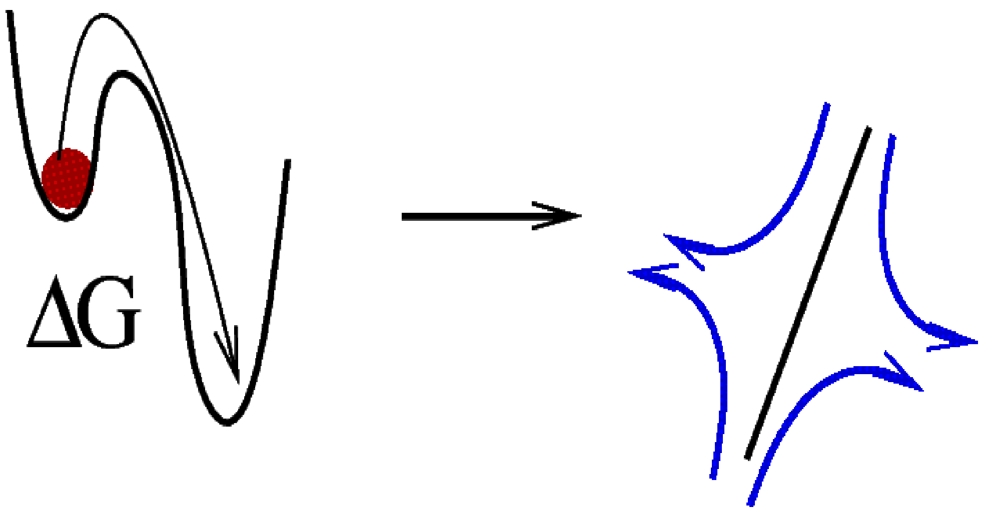
Contractile active particle
PULLER



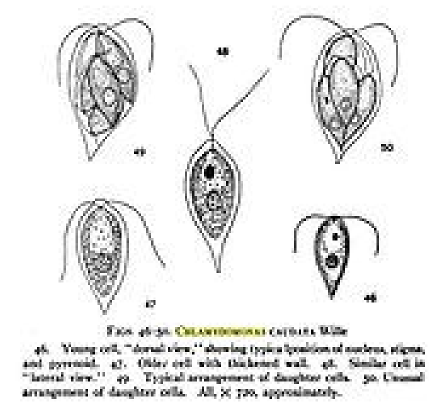
Motor cluster on actin filaments
arXiv:cond-mat/0607287 v1

- Active particles consume free-energy
- Move and stir surrounding medium
- Require no *external* force

Minimal active particle = force dipole



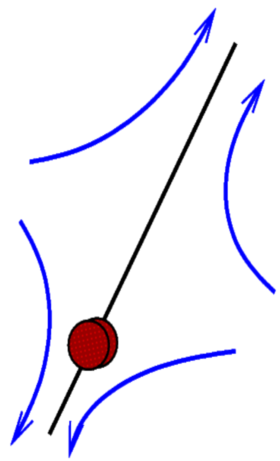
Contractile active particle
PULLER



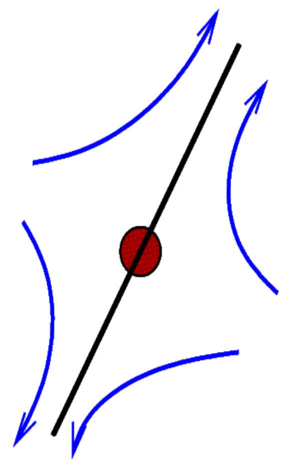
T E Hazen, Bull. Torrey Botan Club. April, 1922, pp. 87-92

- Active particles consume free-energy
- Move and stir surrounding medium
- Require no *external* force

Movers and shakers*



Asymmetric dipole



Symmetric dipole

ORDER PARAMETER

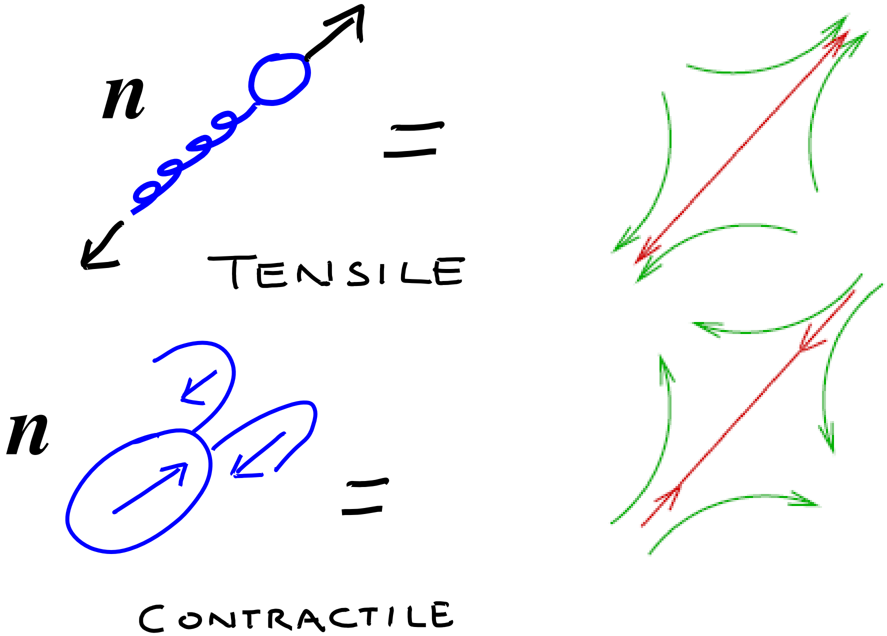
Vector ***p***

Traceless symmetric tensor ***Q***

*M Rao 2004

Self-driven + fluid: active stresses

Simha & SR PRL 2002 order. fluct: Hatwalne *et al.* 2004 rheology



Pedley & Kessler 1992
Prost *et al.* 1995, 2001
Brennen & Winet 1977
Finlayson & Scriven 1969

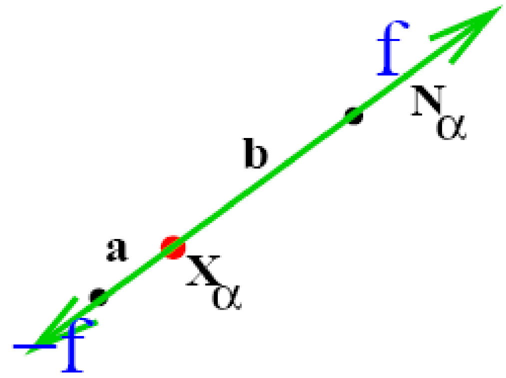
activity ↔ permanent force dipoles

$$\sigma^{a} = K\mathbf{n}\,\mathbf{n}$$

K = constt; $\mathbf{n}$ = local axis
Sgn *K*: contractile/tensile

A *nonequilibrium* effect: *equilibrium* anisotropic fluids have *isotropic* stress (Pascal)

Point-force dipole model



Point forces, equal magnitude, opposite direction

$a \neq b$: mover (polar, vectorial); velocity $\mathbf{v}_\alpha = v_0 \mathbf{N}_\alpha$

$a = b$: shaker (apolar, nematic); velocity $= 0$

Coarse-grain: $\mathbf{v}_\alpha \rightarrow \mathbf{v}(\mathbf{x}, t)$; $\mathbf{v}_\alpha \mathbf{v}_\alpha - \frac{1}{3} v_\alpha^2 \rightarrow \mathbf{Q}(\mathbf{x}, t)$

Liquid-crystal hydrodynamics with a difference

F = free energy relative to isotropic fluid
Tensors **Q** = orientation, $\boldsymbol{\Omega}$ = vorticity, **A** = deformation rate

$$(\partial_t + \mathbf{u}\cdot\nabla)\mathbf{Q} - (\boldsymbol{\Omega}\cdot\mathbf{Q} - \mathbf{Q}\cdot\boldsymbol{\Omega}) = \left[\lambda_0 \mathbf{A} + \lambda_1 \mathbf{A}\cdot\mathbf{Q} - \Gamma\frac{\delta F}{\delta \mathbf{Q}}\right]_{\mathrm{ST}}$$

$$-\eta\nabla^2\mathbf{u} = \nabla\cdot\left[\left(\lambda_0\frac{\delta F}{\delta\mathbf{Q}} - \lambda_1\mathbf{Q}\cdot\frac{\delta F}{\delta\mathbf{Q}}\right)_{\mathrm{ST}} - W_2 c\mathbf{Q}\right] - \nabla p$$

active stress

Simha and SR 2002; Hatwalne *et al.* 2004
Kruse, Juelicher, Joanny, Prost, Voituriez, Sekimoto
Curie/ESPCI/Dresden 2004-present

Liquid-crystal hydrodynamics with a difference

Extensional flow: Orienting torque

Thermodynamic relaxation

Comoving co-rotating derivative

$$(\partial_t + \mathbf{u}\cdot\nabla)\mathbf{Q} - (\boldsymbol{\Omega}\cdot\mathbf{Q} - \mathbf{Q}\cdot\boldsymbol{\Omega}) = \left[\lambda_0\mathbf{A} + \lambda_1\mathbf{A}\cdot\mathbf{Q} - \Gamma\frac{\delta F}{\delta\mathbf{Q}}\right]_{\mathrm{ST}}$$

Symmetrised, traceless

$$-\eta\nabla^2\mathbf{u} = \nabla\cdot\left[\left(\lambda_0\frac{\delta F}{\delta\mathbf{Q}} - \lambda_1\mathbf{Q}\cdot\frac{\delta F}{\delta\mathbf{Q}}\right)_{\mathrm{ST}} - W_2 c\mathbf{Q}\right] - \nabla p$$

Viscosity

pressure

Ericksen stresses

ACTIVE STRESS

Stokesian case: inertia and acceleration ignored

CONSEQUENCES →

Long-wavelength equations of motion

$$\partial_t Q_{xz} = -\frac{\alpha c_0 W_2}{\eta} Q_{xz}$$

Splay instab
if contractile

Growth rate nonzero
for wavenumber → 0

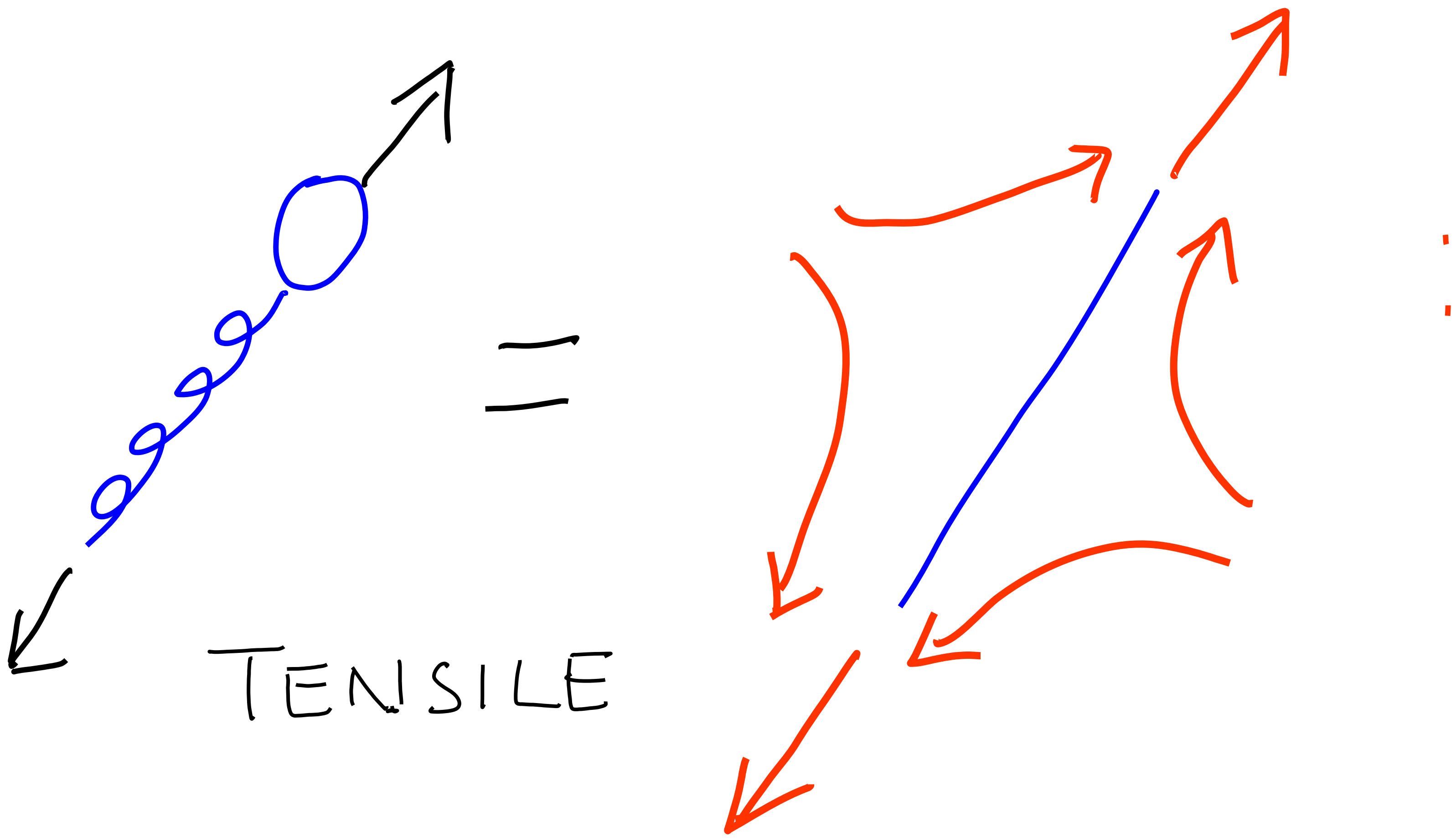
$$\partial_t Q_{xz} = +\frac{\alpha c_0 W_2}{\eta} Q_{xz}$$

Bend instab
if tensile

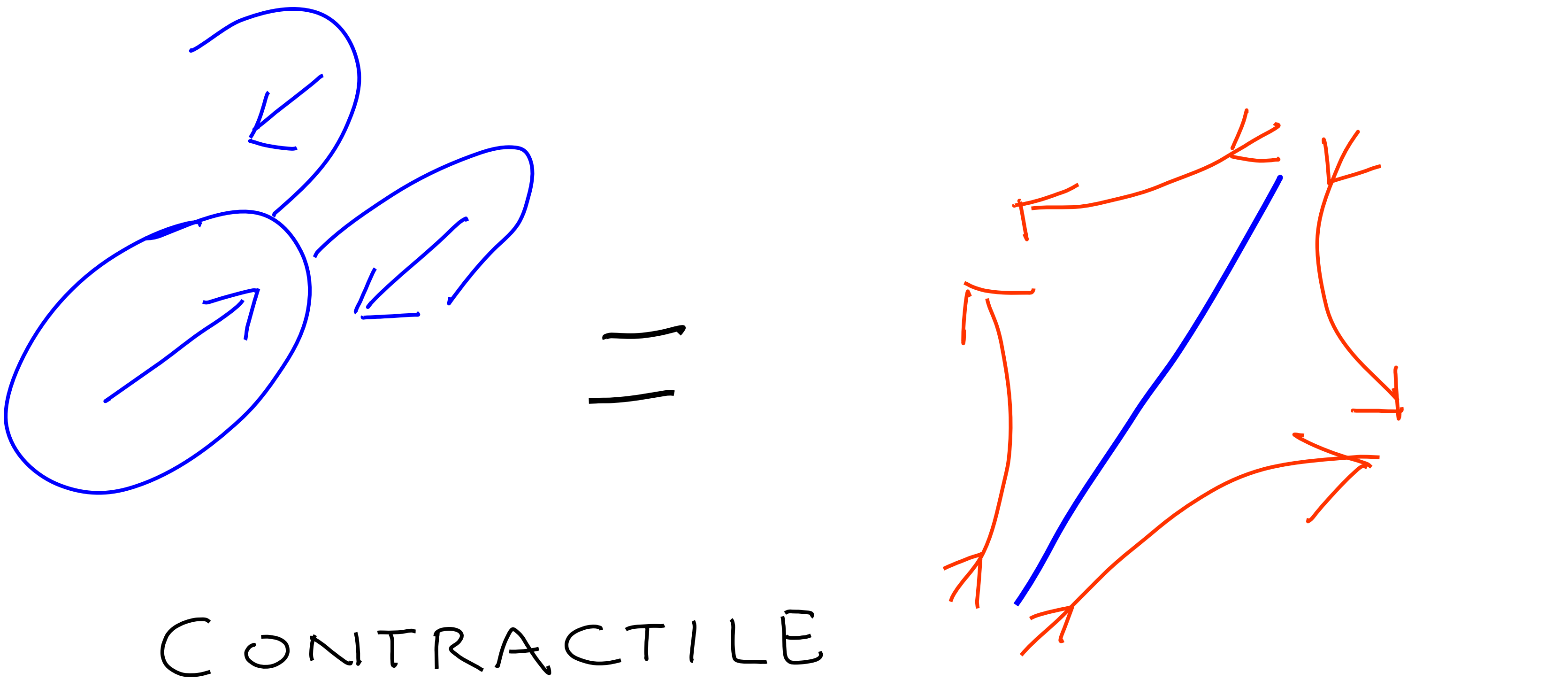
$\alpha > 0$ = flow-director coupling, c_0=conc, η = visc
$W_2 > 0$ = tensile activity; $W_2 < 0$ = contractile activity

Simha-SR 2002; SR-Rao 2007

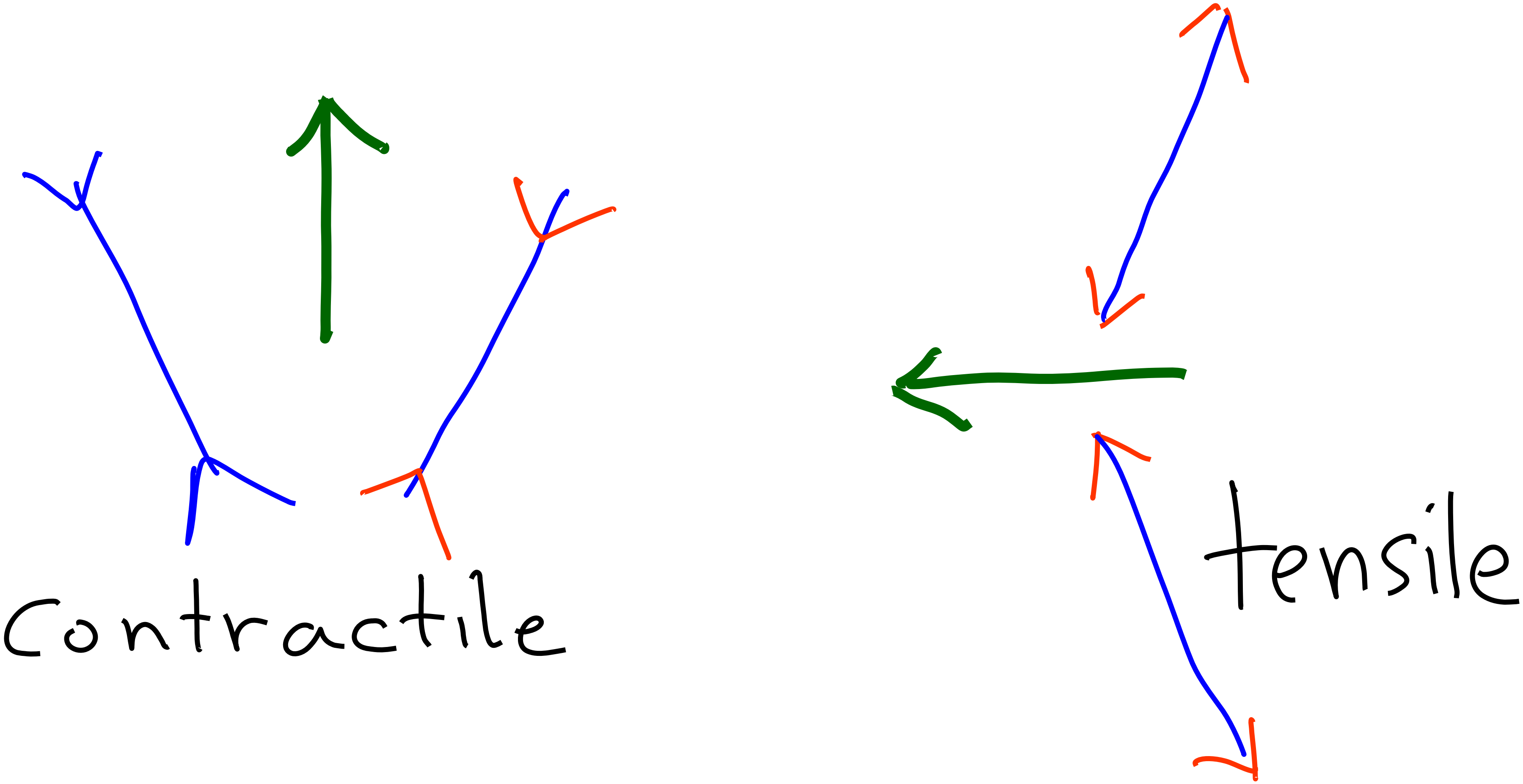
Physical picture



Physical picture

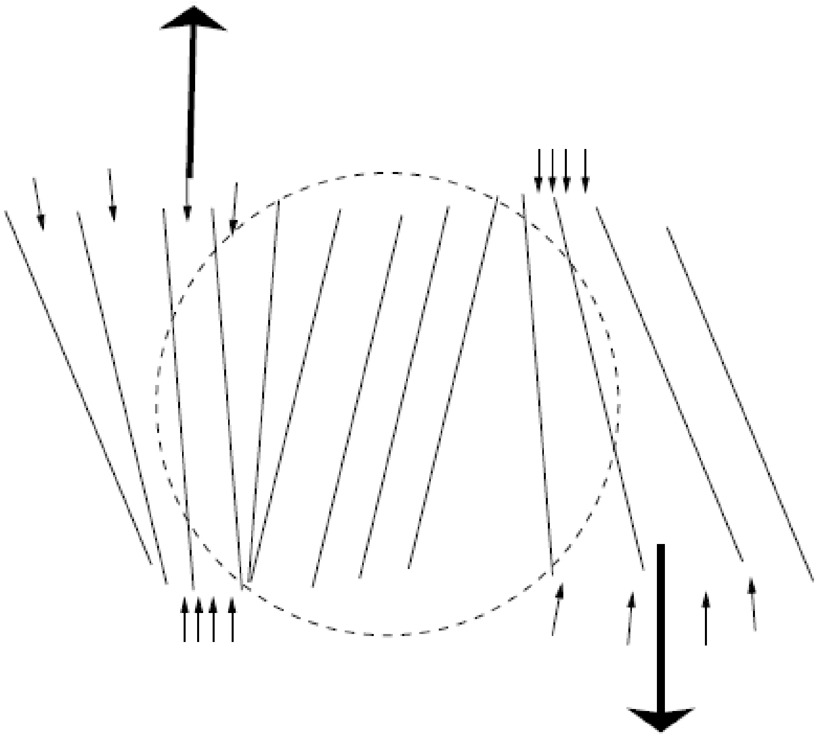


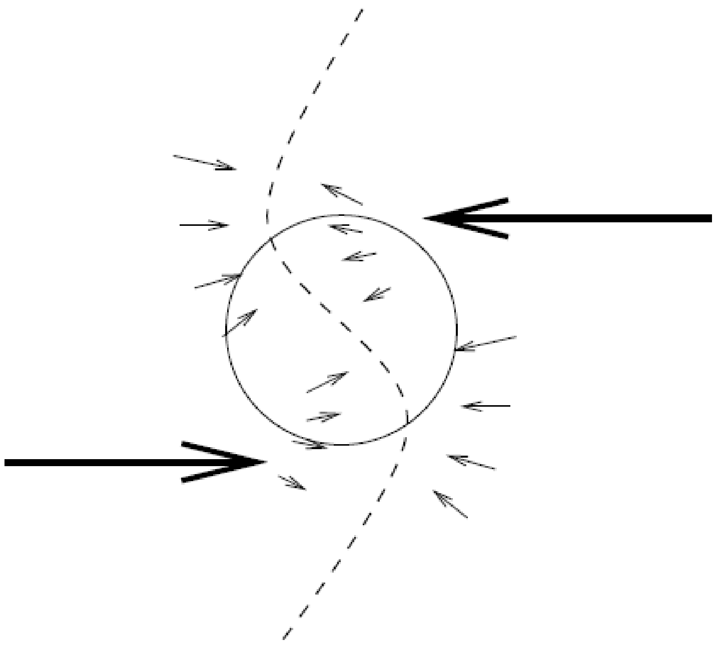
Splay or bend: pump



Curvature → pumping

Splay or bend instability: spontaneous flow

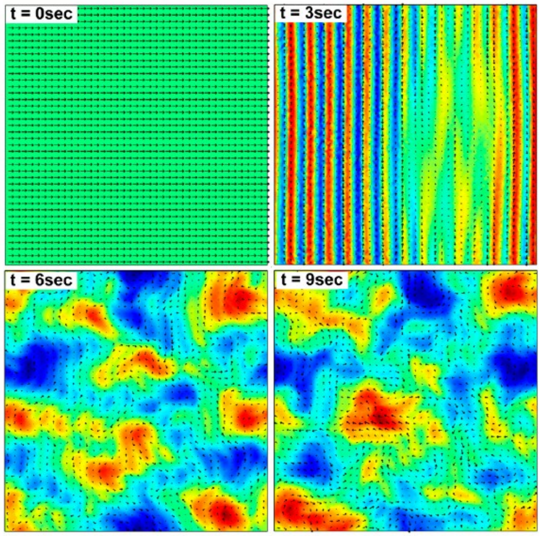




R A Simha & SR PRL 2002, '04
Joanny, Julicher, Kruse, Prost, Voituriez 2004,5,6
SR + Rao NJP 2007

Expts: Dombrowski *et* al. 2005;
Simulations: Saintillan and Shelley 2007
Wolgemuth bacterial turbulence 2008

Bacterial flocks are unstable



Wolgemuth
Biophys J 2008

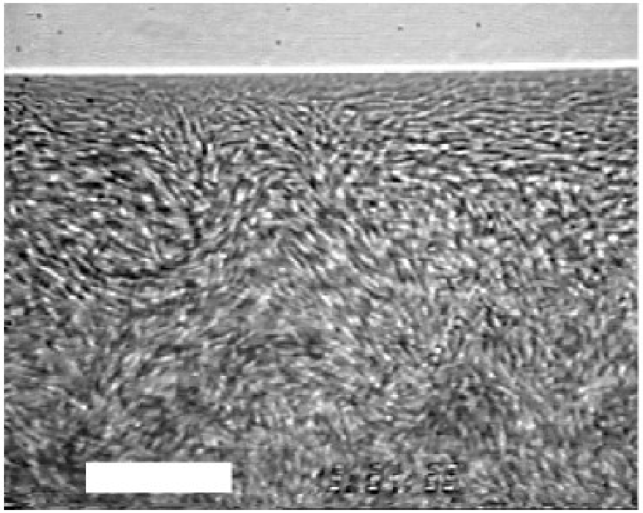


FIG. 3. Bacterial "turbulence" in a sessile drop, viewed from below through the bottom of a petri dish. Gravity is perpendicular to the plane of the picture, and the horizontal white line near the top is the air-water-plastic contact line. The central fuzziness is due to collective motion, not quite captured at the frame rate of $1/30$ s. The scale bar is 35 μm.

Saintillan
and Shelley
PRL 2007-08

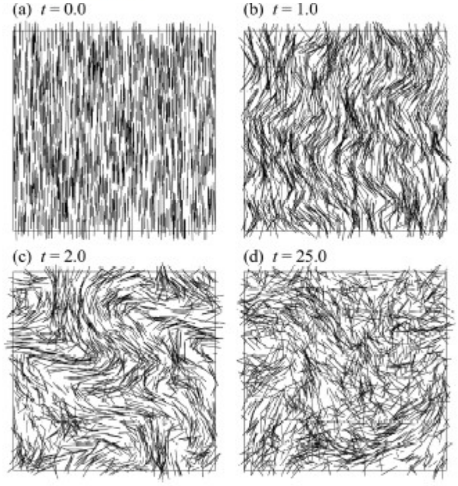


FIG. 1. Orientational instability in a polar nematic suspension of pushers, at an effective volume fraction of $n(L/2)^3 = 1.0$. The figure shows a region of dimensions $10 \times 10 \times 3$ (in units of particle length) containing 2500 particles at different stages of the instability (a)–(d).

Dombrowski et al.
PRL 2005

Orientational Order and Instabilities in Suspensions of Self-Locomoting Rods

David Saintillan and Michael J. Shelley

Hydrodynamic simulation:
thin rods with imposed
surface shear stress

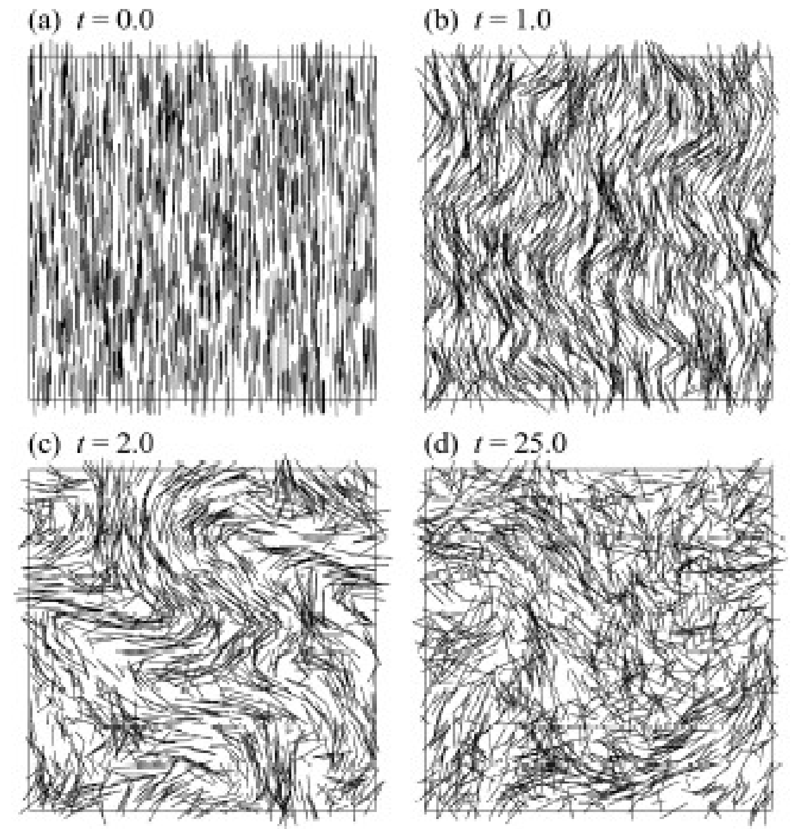


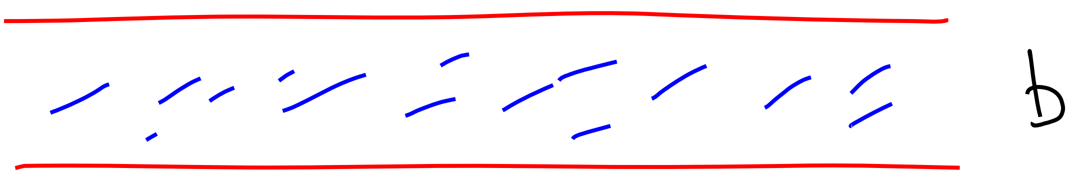
FIG. 1. Orientational instability in a polar nematic suspension of pushers, at an effective volume fraction of $n(L/2)^3 = 1.0$. The figure shows a region of dimensions $10 \times 10 \times 3$ (in units of particle length) containing 2500 particles at different stages of the instability (a)–(d).

Direct test confirms
our predicted instability

More on instabilities:
Marenduzzo *et al.* 2005
Fielding *et al.* 2008

Suppressing the instability: finite size

SR and M. Rao, New J Phys 2007
(physics of the cytoskeleton)

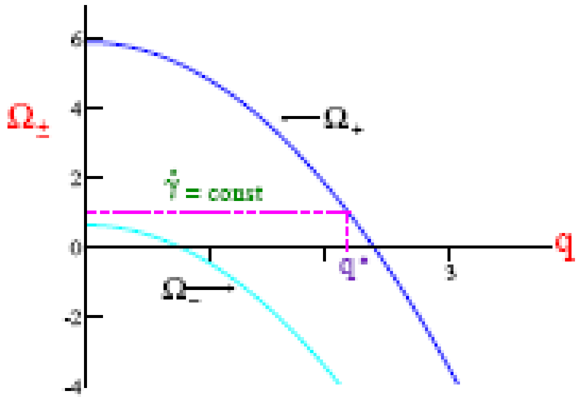


$$\partial_t Q_{xz} = -\left[\frac{\alpha c_0 W_2}{q_x^2 + (\pi/b)^2} + K\right]\frac{q_x^2}{\eta} Q_{xz}$$

- K = Frank elastic constant of underlying nematic
- Stable if b small enough
- Fix b, increase W_2 -- diffusive instability
- Final state: Modulated? Turbulent? M Graham *et al* 2008

Need nonlinearities

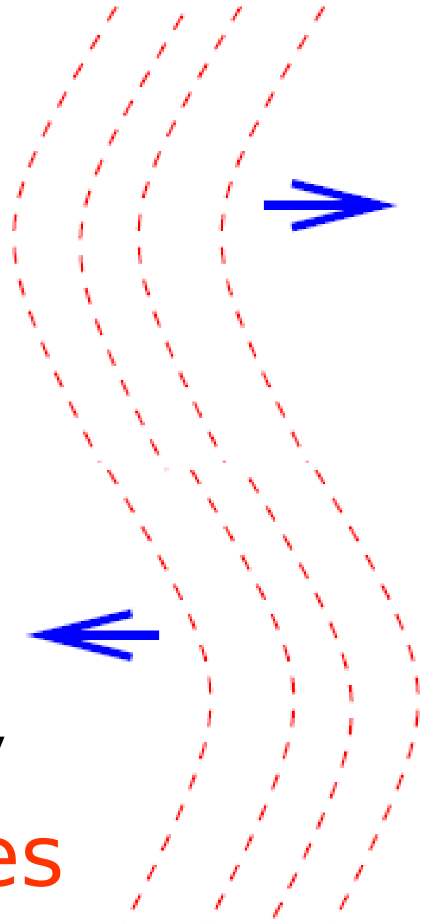
Suppressing the instability: shear

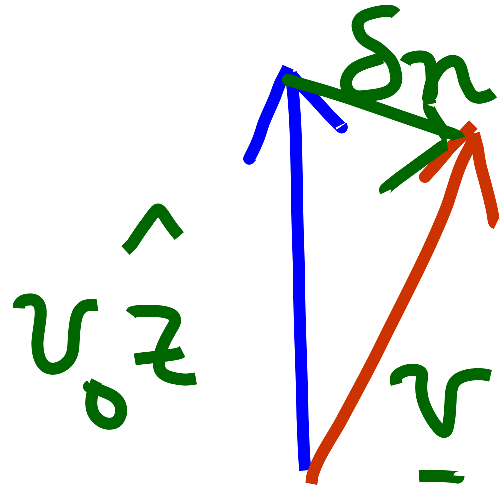


Muhuri *et al.* EPL 2007
Impose shear: shear-rate > unperturbed growth rate
→stabilised state – can talk meaningfully of rheology
Further developments: Fielding *et al.* 2008

Ordered phase of fish

$$\mathbf{v} = v_0\hat{\mathbf{z}} + \delta\mathbf{n}$$





Curvature → flow

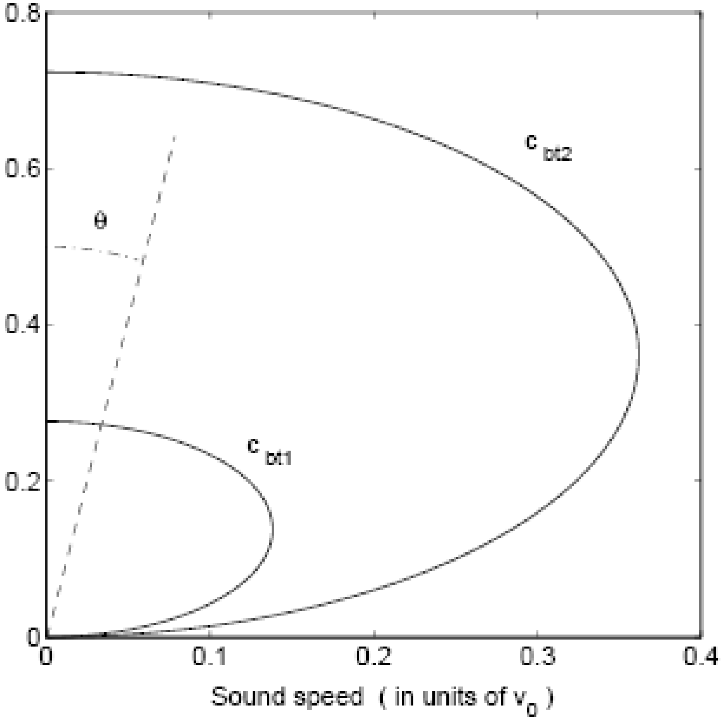
Shear rotates $\mathbf{v}$

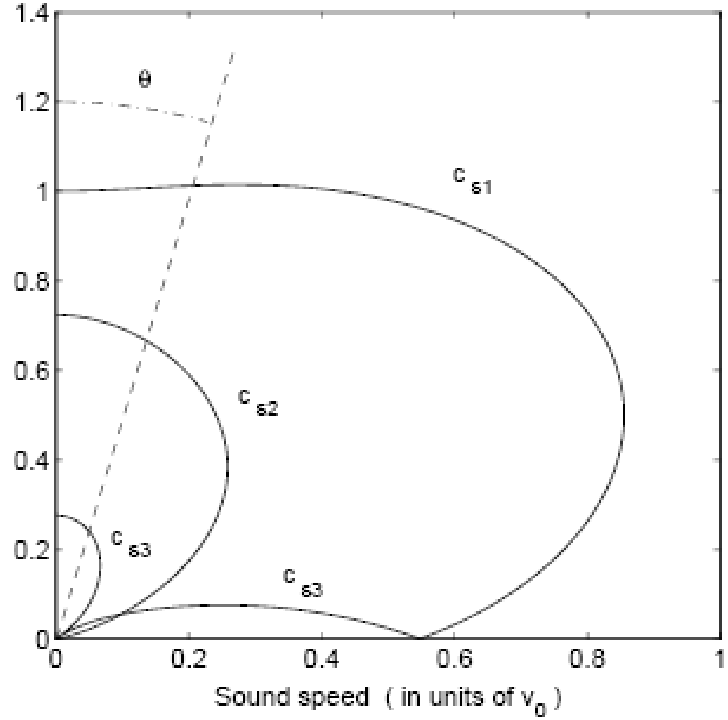
Simha-SR
PRL 2002

Inertia → splay
and bend waves

Fish waves: Makris et al., Science 2006

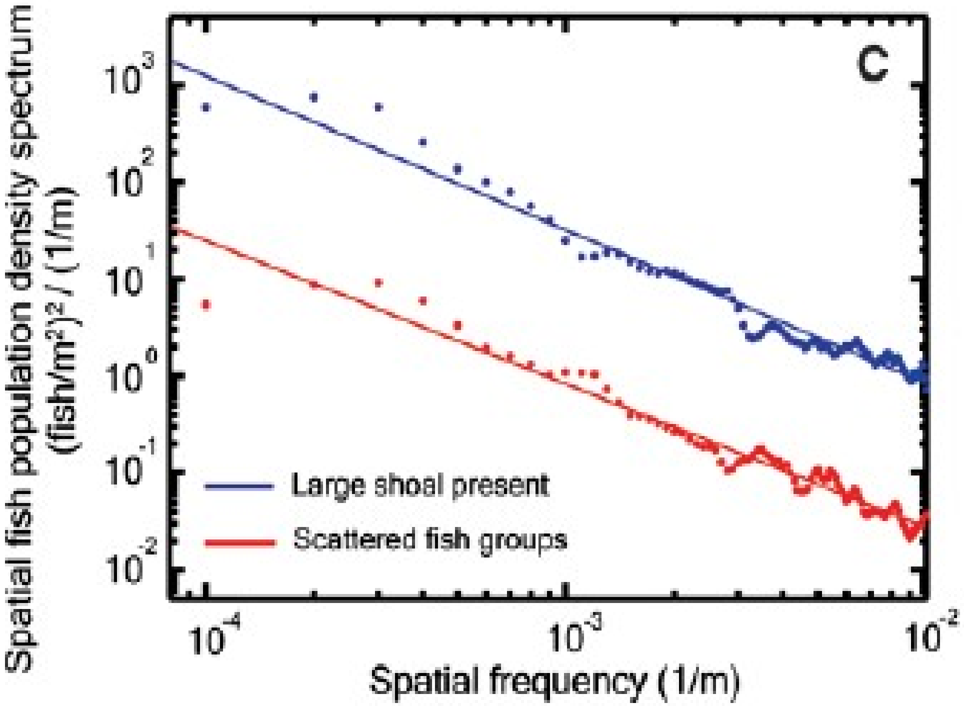
Large scales -- fish: inertia dominates





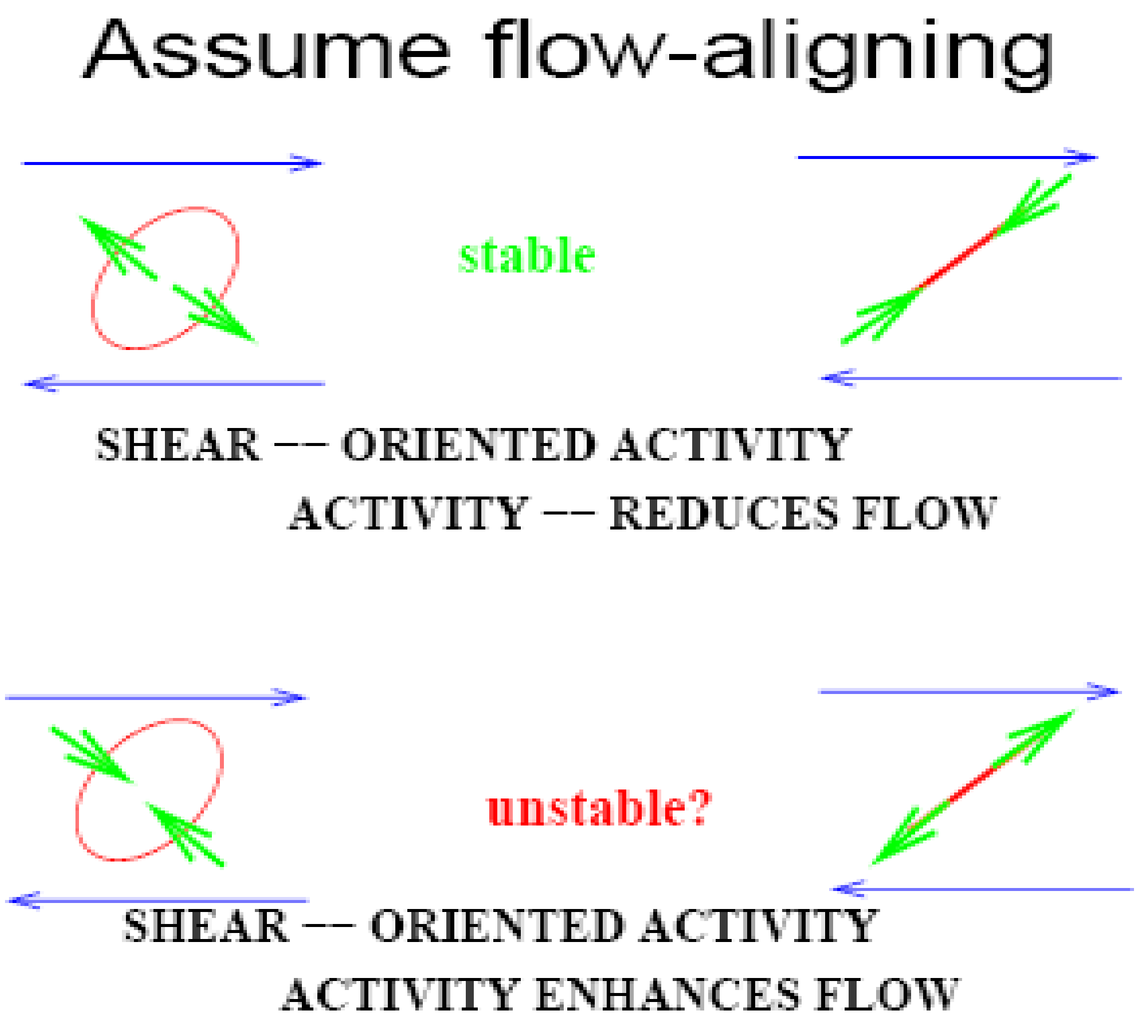
Polar order: propagating modes
Giant density fluctuations a la Toner-Tu
Simha + SR PRL 2002

Structure factor of fish shoal



Makris et al. Science **311** (2006) 660
Also report: propagating modes

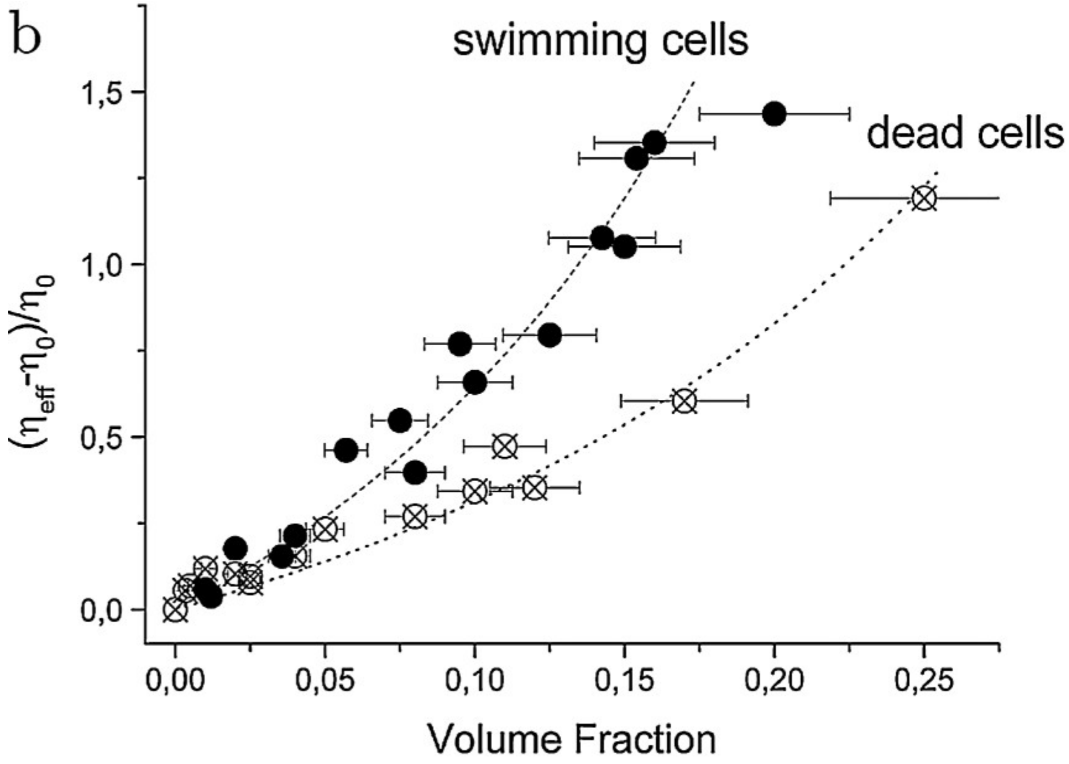
Active rheology: isotropic phase



Hatwalne *et al.* PRL 2004

Experiments: swimming affects viscosity

Theory: Hatwalne *et al.* 2004
Contractile rods increase viscosity
Extensile rods decrease viscosity



Rafai et al., PRL **104** (2010) 098102
chlamys more viscous alive than dead
Our effect? Gravity torques?

http://focus.aps.org/story/v25/st9

Experiments: swimming affects viscosity

Sokolov & Aranson
PRL **103** (2009) 148101
B subtilis: less viscous alive than dead

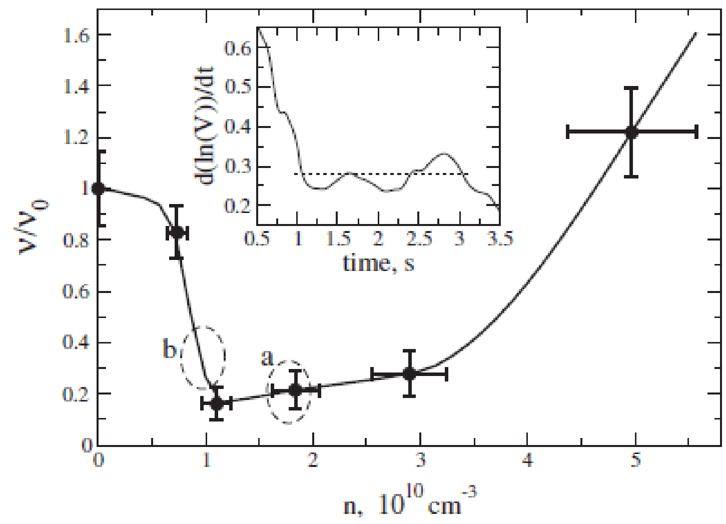


FIG. 3. Viscosity for 6 different concentrations of bacteria. ν_0 is the viscosity of the liquid without bacteria. Inset: instant viscosity vs time during decay of the vortex for density $n = 2.9 \times 10^{10}$. The dashed line is the average value of the viscosity during the slow phase of decay. See movies 1 and 2 in [19].

Active orientational ordering is like a glass transition

- Contractile filaments, confined
- Approach transition to orientational order
- Relaxation time τ increases
- Viscosity grows $\sim\tau$: strong viscoelasticity
- Active nematic has yield stress, rigidity

Hatwalne *et al.* 2004
Liverpool-Marchetti 2007
Fielding *et al.* 2008

Details -->

$$\rho(\partial_t + \mathbf{u}\cdot\nabla)\mathbf{u} = -\nabla\cdot(\sigma^a + \sigma^b) - \eta\nabla^2\mathbf{u} - \nabla\Pi$$

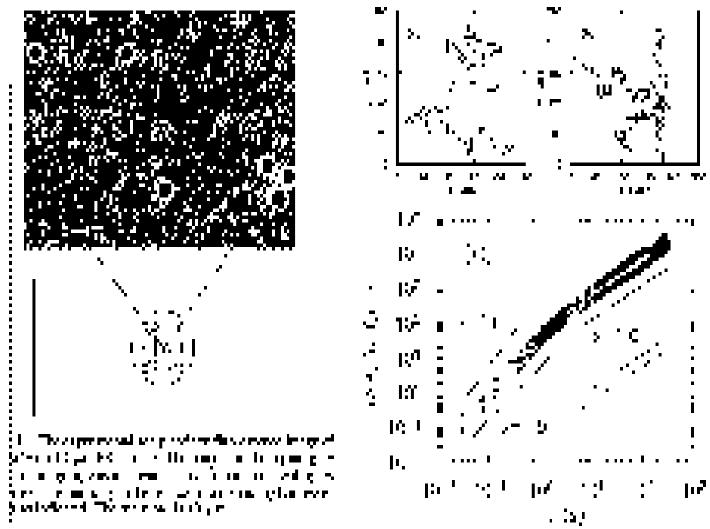
$$\boldsymbol{\sigma}^{\mathrm{a}} - (1/3)\mathbf{I}\,\mathrm{Tr}\,\boldsymbol{\sigma}^a = W\mathbf{Q}$$

$$\frac{\partial \mathbf{Q}}{\partial t} = -\frac{1}{\tau}\mathbf{Q} + D\nabla^2\mathbf{Q} + \lambda_0\mathbf{A} + \cdots + \mathbf{f},$$

$$\sigma_{xy}(\omega) = -\left[\eta_0 + \frac{(a+W)\lambda_0}{-i\omega + \tau^{-1}}\right]A_{xy}$$

$$\equiv -\frac{G'(\omega) - iG''(\omega)}{\omega}\,iA_{xy},$$

Tracer diffusion in an active fluid



Giant effective temperature: Wu-Libchaber PRL 2000
Bacterial swimming enhances colloid diffusion by 10^3

Theory? -->

Tracer diffusion in an active fluid

typical speed u_0

correlated over a scale ξ and time τ

$\boldsymbol{\sigma}^a(k=0,\omega=0)$ is $\sim W^2\xi^3\tau$ $\qquad W \sim \eta u_0/\xi$

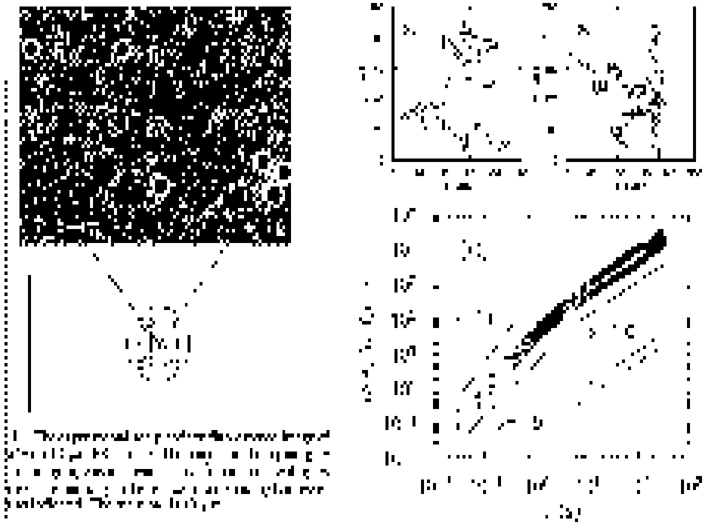
equating this stress variance to $k_B T_{\text{eff}}\eta$

swimming speed $\sim$20 μm/s, and $\tau \sim 1$ s

$T_{eff} \sim 10^5$–10^6 K

Hatwalne et al. PRL 2004

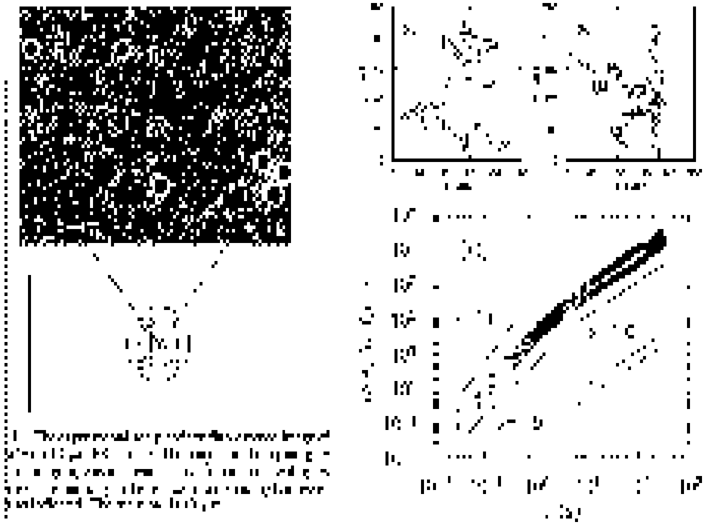
Tracer diffusion in an active fluid



Giant effective temperature: Wu-Libchaber PRL 2000

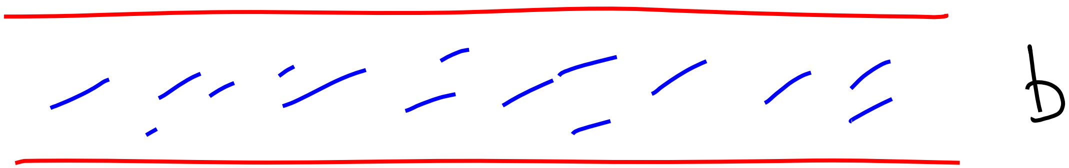
Bacterial swimming enhances colloid diffusion by 10^3

Tracer diffusion in an active fluid



Giant effective temperature: Wu-Libchaber PRL 2000
Bacterial swimming enhances colloid diffusion by 10^3

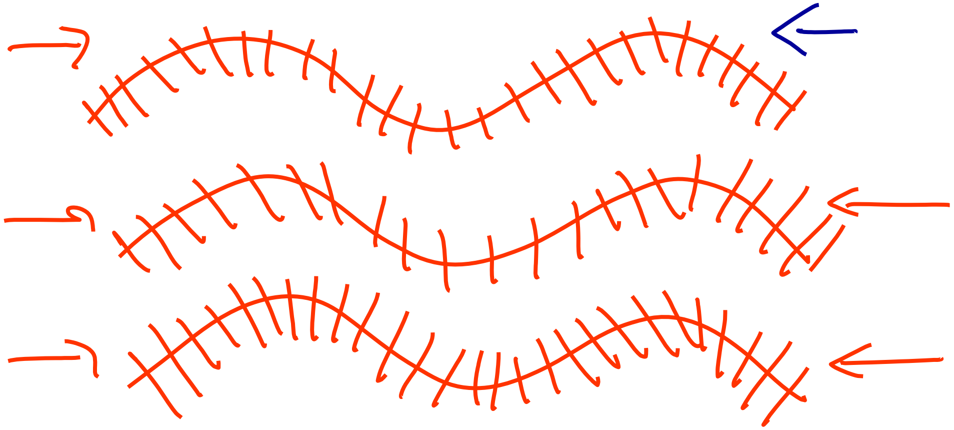
A weird yield-stress material

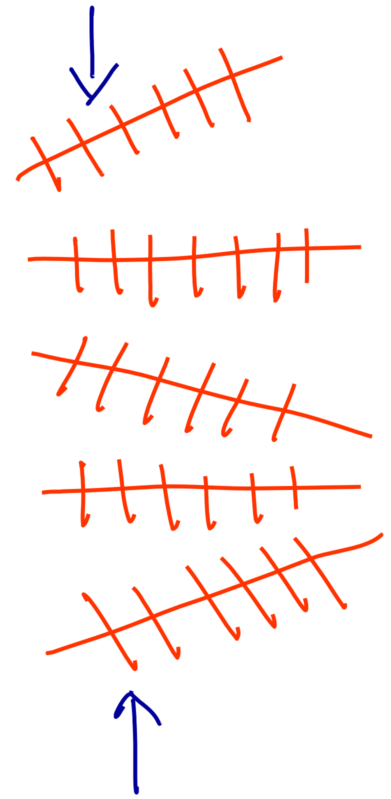


- b small enough: no instability
- Stably flow-aligning: filaments line up at an angle
- Stress proportional to Q: yield stress!
- Apply shear along different principal axes: flows!
- Like fragile jammed granular matter?

SR + Madan Rao New J Phys 2007

Suppressing the instability: lamellar order

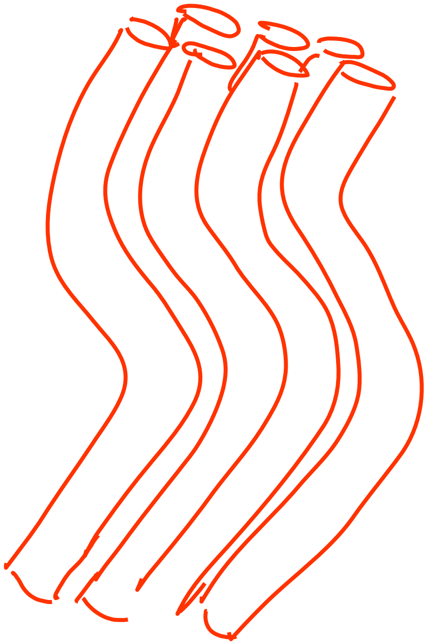


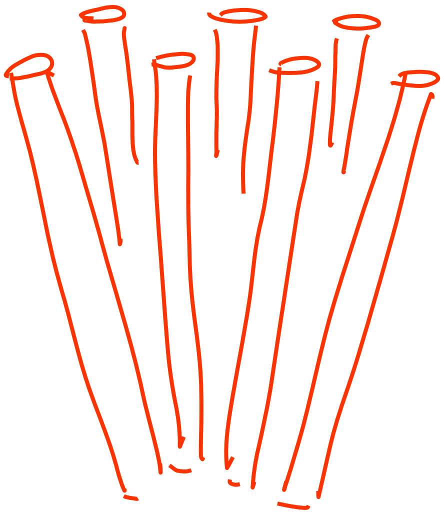


Contractile still splay-unstable
Bend instab of tensile suppressed if modulus strong enough

SR and M. Rao, New J Phys 2007
(physics of the cytoskeleton)

Suppressing the instability: columnar order



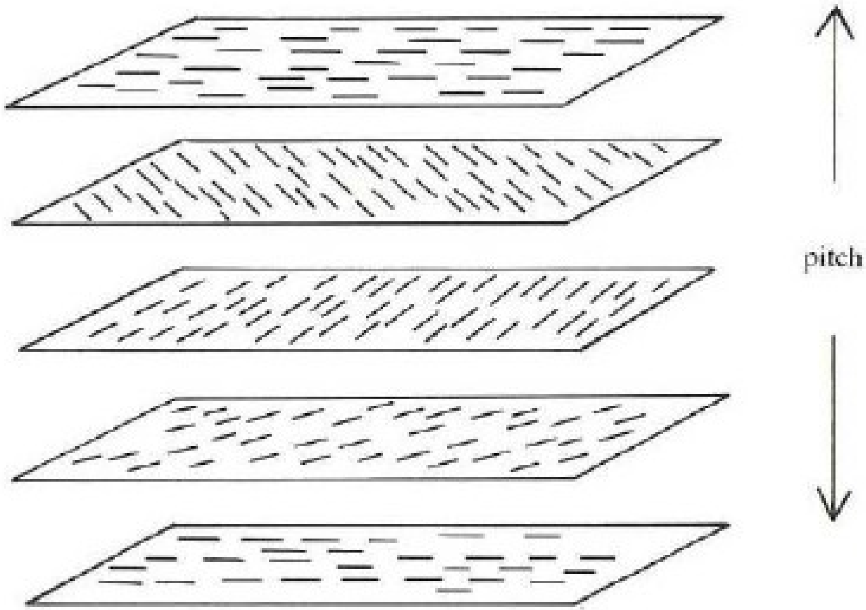


Tensile still bend-unstable
Splay instab of contractile suppressed
if modulus strong enough

Analogous results
for cholesteric order:
T Adhyapak, D Marenduzzo, SR

SR and M. Rao, New J Phys 2007
(physics of the cytoskeleton)

Orientational order + chirality → cholesteric



Biofilaments are chiral:
Interplay of cholesteric elasticity and active instability?

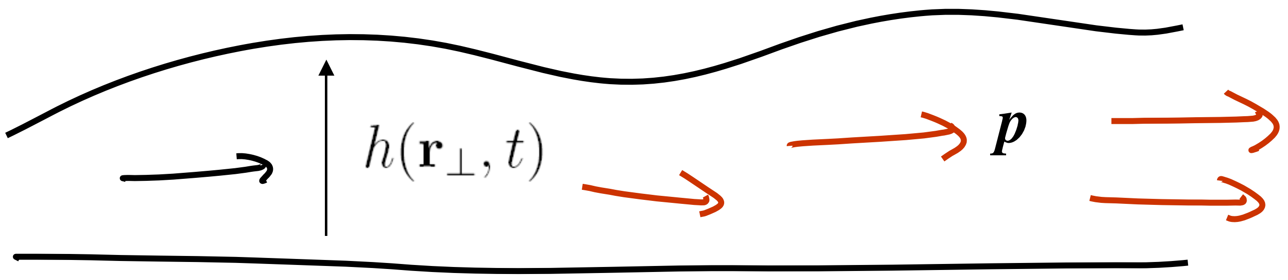
T Adhyapak, D Marenduzzo

Cholesteric elasticity expels layer splay, supresses instability of contractile active filaments

$$\omega = -iK_3 \left(\frac{(1+\nu)^2}{4\eta} + \frac{1}{\gamma} \right) q_0^2 - i \frac{(1+\nu)\zeta\Delta\mu}{2\eta}$$

Instabilities of active ordered thin film

Background:
H. Stone,
Cargese
Notes;
Oron *et al.*
RMP 1997



Slow variables:
height field h
polar order parameter $\boldsymbol{p}$
concentration c

Free surface:
spontaneous splay;
order parameter couples to tilt

Inside film: viscous and active forces balance
eliminate hydro velocity in favour of c, h, $\boldsymbol{p}$

S Sankararaman + SR
arXiv:0809.4918

$$\partial_t h = -\nabla \cdot (h\mathbf{M} \cdot \boldsymbol{\nabla} \cdot \boldsymbol{\sigma})$$

Active thin-film equations

polarization vector $\mathbf{p} = (\mathbf{p}_\perp, p_z)$

concentration field c

hydrodynamic velocity field $\mathbf{u} = (\mathbf{u}_\perp, u_z)$

height field $h(\mathbf{r}_\perp, t)$ of the film

Incompressibility
$$\dot{h} + \nabla_\perp \cdot \int_0^h \mathbf{u}_\perp dz = 0$$

Stokes equation

lubrication
$$\mu \partial_z^2 \mathbf{u}_\perp - \nabla_\perp P - \hat{z}\partial_z P - \nabla \cdot \sigma^{\mathbf{a}} = 0$$

pressure

active stress

express $\mathbf{u}_\perp$ in terms of $\mathbf{p}$, c and h

Thin-film dynamics

$$\mathbf{p} \cdot \hat{N} = 0 \text{ where } \hat{N} = (-\nabla_\perp h, 1)/\sqrt{1 + (\nabla_\perp \mathbf{h})^2}$$

$$\text{Thus } p_z \simeq \mathbf{p}_\perp \cdot \nabla_\perp h \text{ at the free surface}$$

$$p_z = 0 \text{ at the substrate}$$

$$z\text{-averaged description } p_z = (1/2)\partial_x h \text{ and } \partial_z p_z \simeq h^{-1} \partial_x h$$

$$\partial_t \theta = -\frac{i\Gamma C}{h_0} k_y \delta h_\mathbf{k} - \left(D_+ k_x^2 + D_- k_y^2 + i\lambda_1 p_0 k_x \right) \theta - (i\zeta k_y - \Phi k_x k_y)\delta c$$

$$\partial_t \delta h_\mathbf{k} = -\frac{afc_0 p_0^2 h_0^2}{3\mu}[2h_0 k_x k_y \theta_\mathbf{k} + h_0 k_x^2 \frac{\delta c_\mathbf{k}}{c_0} + (1 - \frac{1}{2} h_0^2 k_\perp^2) k_x^2 \delta h_\mathbf{k}] - \frac{\gamma h_0^3}{3\mu} k_\perp^4 \delta h_\mathbf{k}$$

$$\partial_t \delta c = -\nabla \cdot [(\mathbf{u} + \lambda_0 \mathbf{p}) c]$$

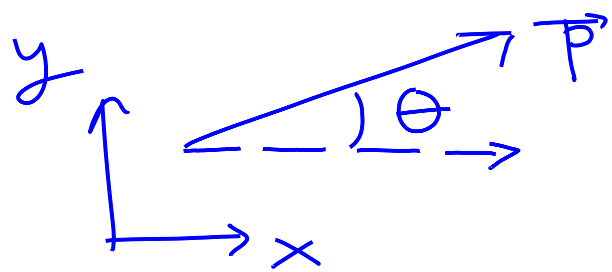
Thin-film dynamics

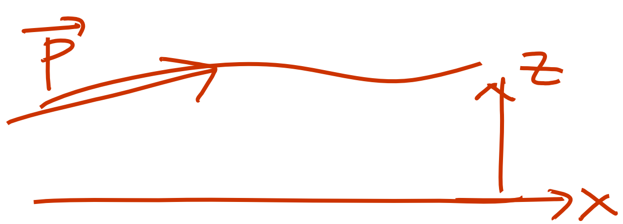
$$\mathbf{p}\cdot\hat{N} = 0 \text{ where } \hat{N} = (-\nabla_\perp h, 1)/\sqrt{1+(\nabla_\perp \mathbf{h})^2}$$

Thus $p_z \simeq \mathbf{p}_\perp \cdot \nabla_\perp h$ at the free surface $\quad$ $p_z = 0$ at the substrate

z-averaged description $p_z = (1/2)\partial_x h$ and $\partial_z p_z \simeq h^{-1}\partial_x h$

$$\mathbf{p}_\perp = p_0\hat{x} + p_0\theta\hat{y},\ \theta \ll 1$$





Thin-film dynamics essentials

$$\partial_t h \sim \sigma_0 \partial_x \partial_y \theta + \cdots$$

Curvature → flow

$$\partial_t \theta + v_0 \partial_x \theta \sim \partial_y h + \cdots$$

Mean drift advects orientation

Tilt rotates polar order parameter

Thin-film mode structure

Depending on signs of coefficients,
this leads as promised to waves with:

$$k_y k_x^{1/2} \text{ for } k_x \ll \xi k_y^2$$

Growth rate at wavevector $\boldsymbol{k} = (k_x, k_y)$

$$k_y^2 \text{ for } k_x \gg \xi k_y^2$$

$\xi \sim$ activity x orientation-tilt coupling/(drift-vel)^2

Thin-film mode structure

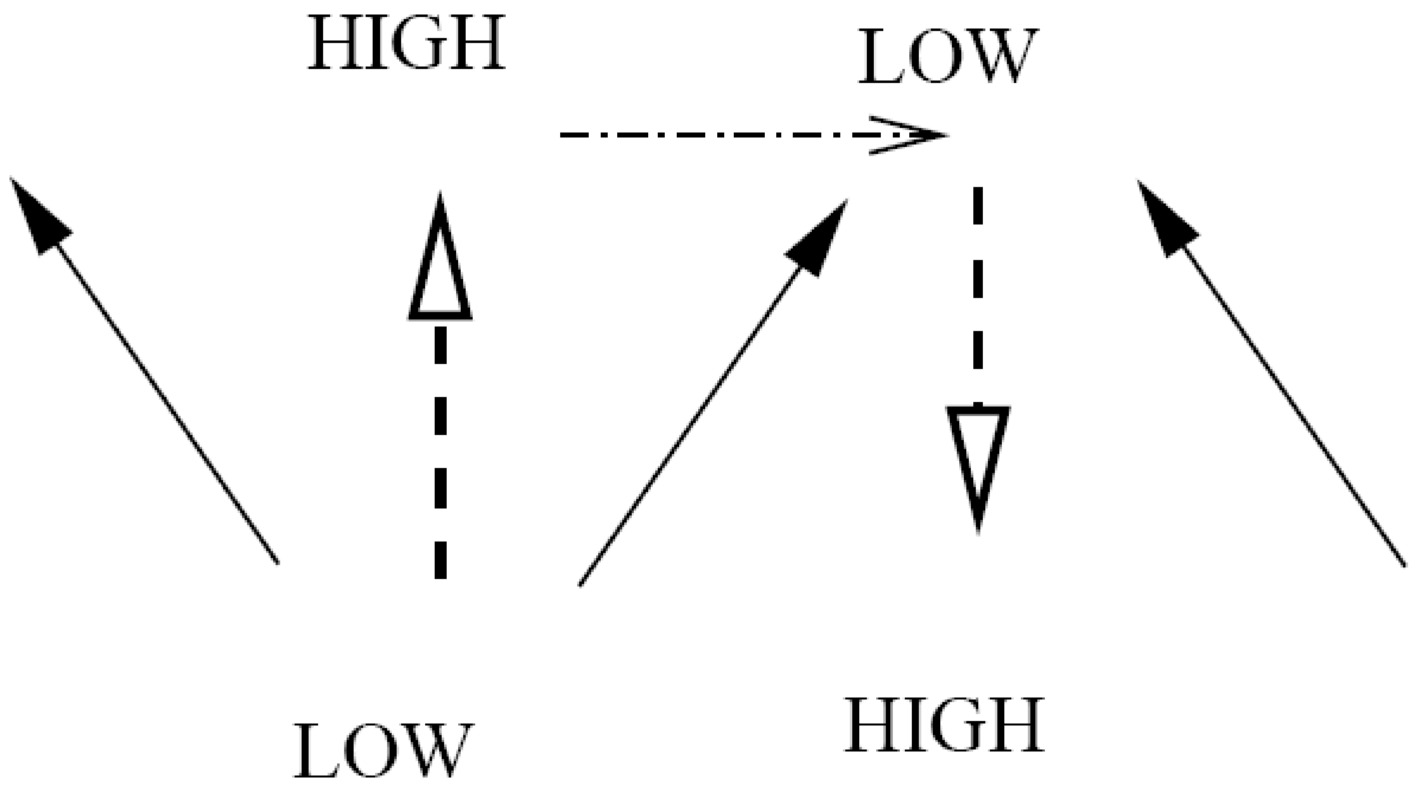
$$k_y k_x^{1/2} \text{ for } k_x \ll \xi k_y^2$$

Growth rate at wavevector $\boldsymbol{k} = (k_x, k_y)$

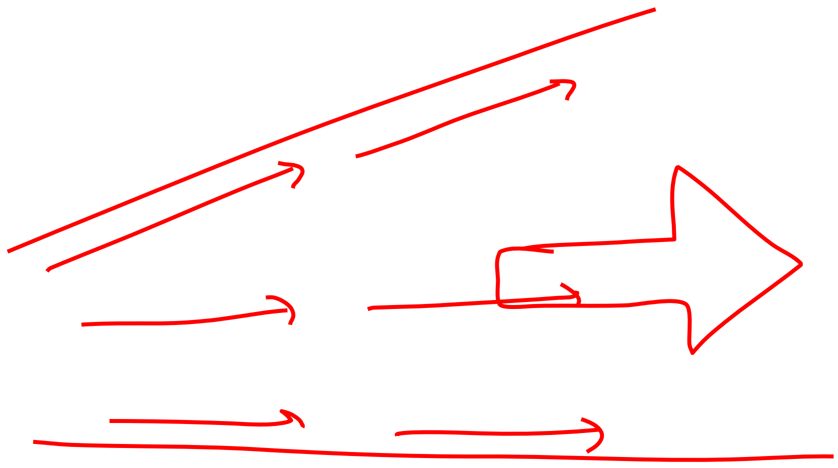
$$k_y^2 \text{ for } k_x \gg \xi k_y^2$$

$\xi \sim$ activity x orientation-tilt coupling/(drift-vel)^2

Instability mechanism



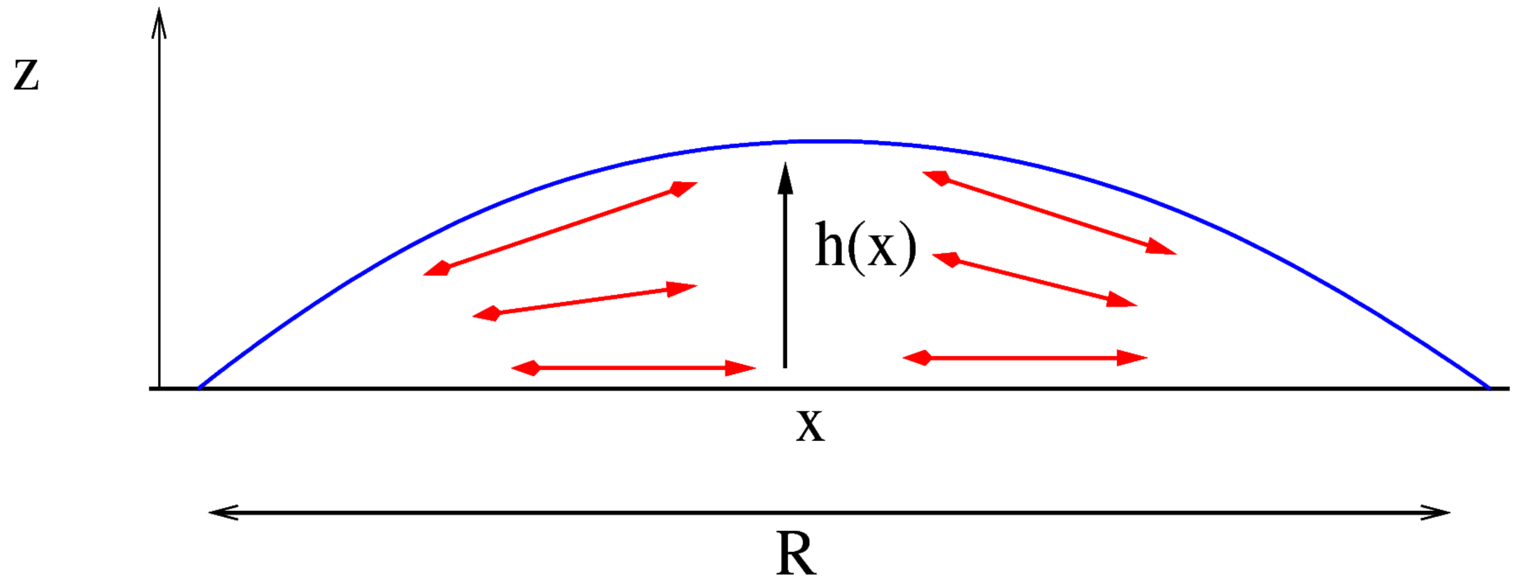
Contractile instability: tilt-induced pumping



Contractile filaments: splay → flow
Free surface unstable

Active drop on a surface

Joanny and SR 2010



Activity strength W
Order parameter ***p***
Polarity unimportant

$$p_z(z=h)=\partial_x h$$

$$p_z(z=0)=0$$

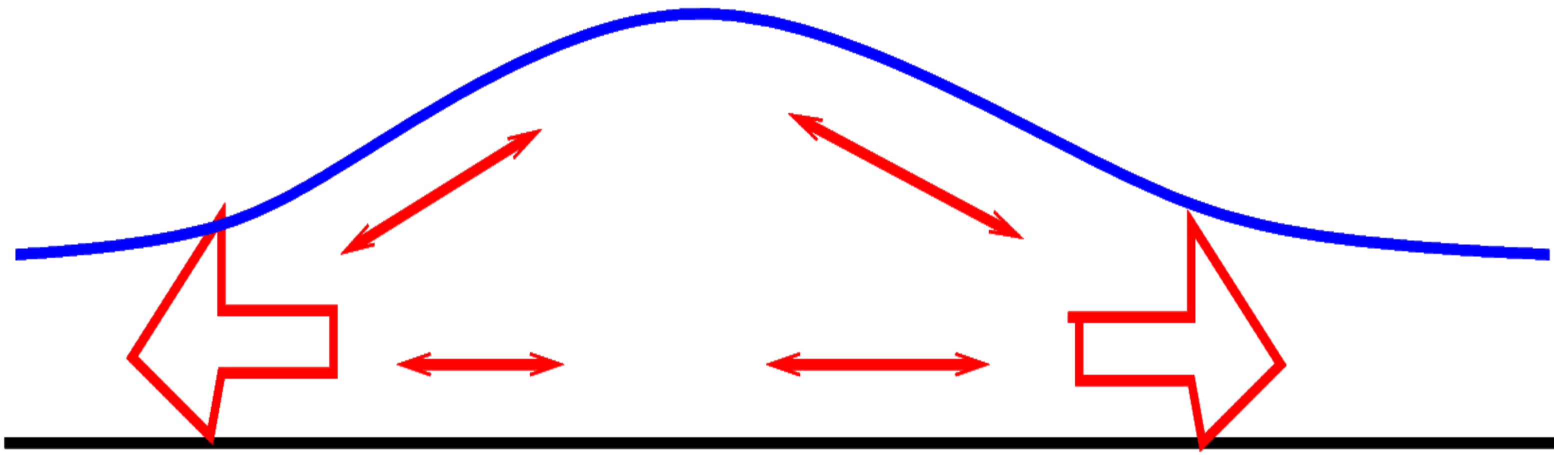
$$p_z(z)=(z/h)\partial_x h$$

$$\sigma^a_{zx}=W p_z p_x \simeq W(z/h)\partial_x h$$

$$\partial_z \sigma^a_{zx} \simeq (W/h)\partial_x h$$

Funny surface pressure gradient

Active spreading



Splayed extensile active stresses promote spreading

Extensile: new spreading law

$$\partial_t h = -\nabla \cdot (h\mathbf{v}) \qquad \mathbf{v} = \frac{h^2}{3\eta}\nabla \cdot \sigma$$

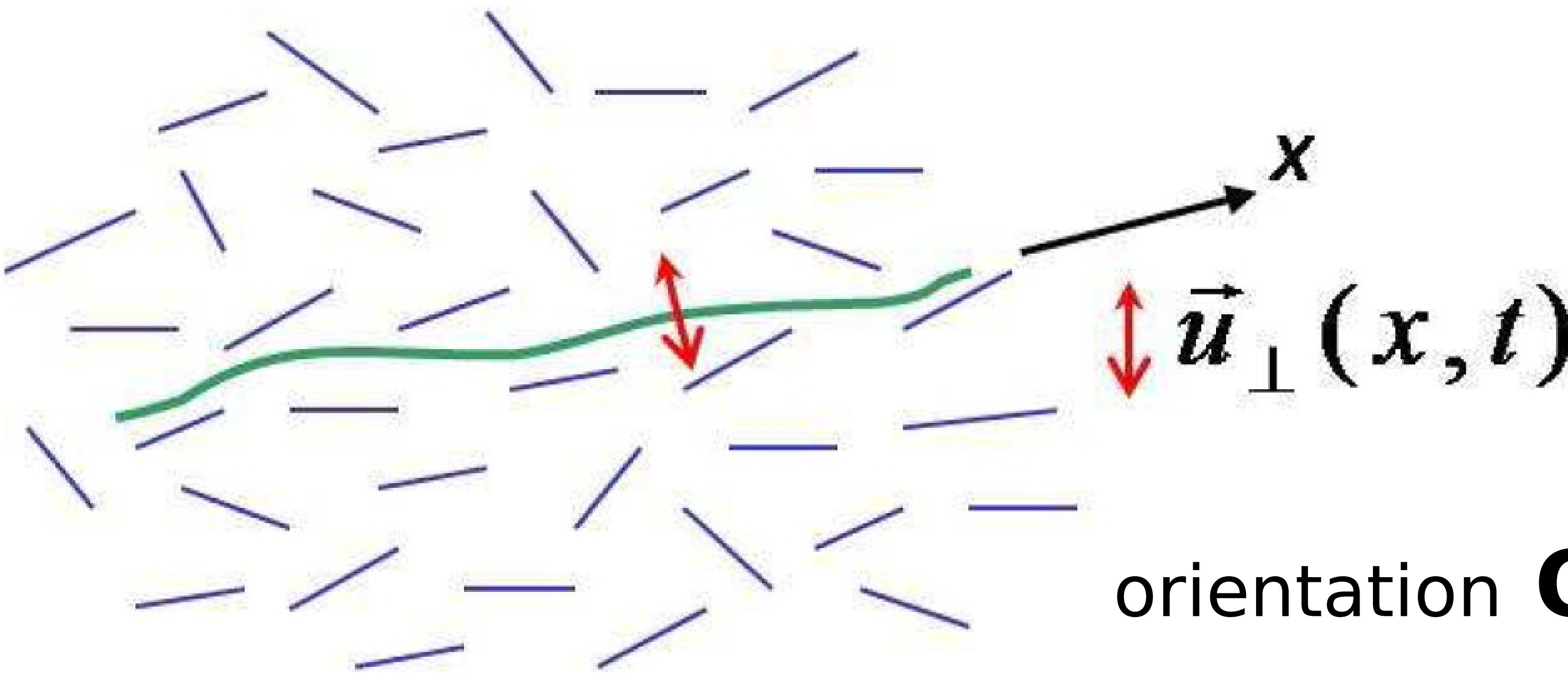
$$\partial_t h = \frac{W}{3\eta}\partial_x(h^2\partial_x h)$$

$$hR^2 = \mathrm{constt}$$

$$R \sim t^{1/6}$$

Joanny SR 2010

A filament in an active medium



orientation **Q**

What happens to a stiff filament surrounded by activity?
How does actin-myosin activity affect microtubules?

Kikuchi *et al.* 2008

A simple model

$$\partial_t \mathbf{u}_\perp - \mathbf{v}_\perp(x, \mathbf{r}_\perp = \mathbf{0}, t) \;=\; -\frac{1}{\gamma}\delta F/\delta \mathbf{u}_\perp + \mathbf{f}_\perp$$

$$\partial_t \mathbf{Q} = \;-\frac{1}{\zeta}\delta F/\delta \mathbf{Q} + \boldsymbol{\eta},$$

$\mathbf{u}_\perp(x,t)$ transverse fluctuations

$\mathbf{v}$ hydrodynamic velocity field

$\mathbf{Q}$ nematic order parameter

$F[\mathbf{u}_\perp, \mathbf{Q}]$ free-energy functional

Free-energy: ordering, elasticity, anchoring

$$F[\mathbf{u}_\perp, \mathbf{Q}] = F_f[\mathbf{u}_\perp] + F_{LD}[\mathbf{Q}] + F_{anc}[\mathbf{u}_\perp, \mathbf{Q}]$$

$$F_f[\mathbf{u}_\perp] = \int_0^L dx[(\sigma/2)\,(\partial_x \mathbf{u}_\perp)^2 + (\kappa/2)(\partial_x^2 \mathbf{u}_\perp)^2]$$

$$F_{LD}[\mathbf{Q}] = \int dx \int d^2 r_\perp [(a/2)\mathbf{Q}^2 + (K/2)(\nabla \mathbf{Q})^2]$$

$F_{anc}[\mathbf{u}_\perp, \mathbf{Q}]$ Favours normal or parallel alignment of medium and filament

Where's activity?

$$\mathbf{v}_\perp(x, \mathbf{r}_\perp, t) = -(W c_0/\Gamma)\partial_x \mathbf{Q}_{x\perp}(x, \mathbf{r}_\perp, t)$$

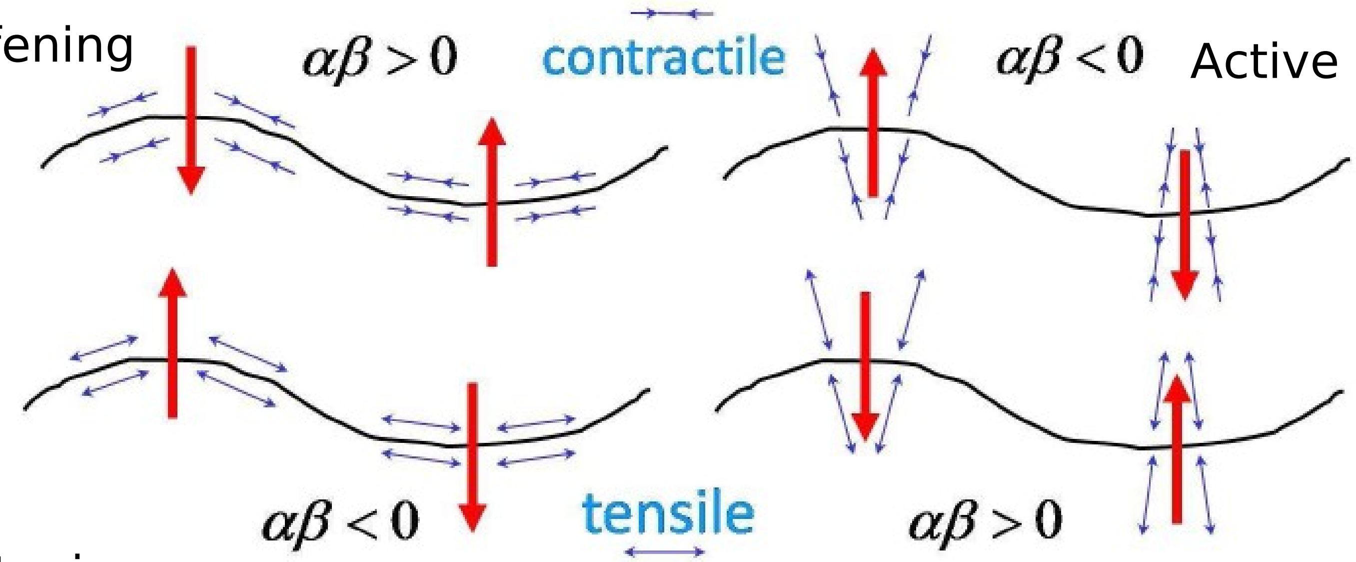
Force balance: friction against active stresses
"Rouse" approximation: local damping

Combine these elements

Interplay: anchoring and activity

Active stiffening

Active softening



Active softening

Active stiffening

- Stiffening: strictly nonequilibrium effect
- At equilibrium, coupling to additional degree of freedom always reduces elastic constant
- Buckling: provides basis for Brangwynne *et al*

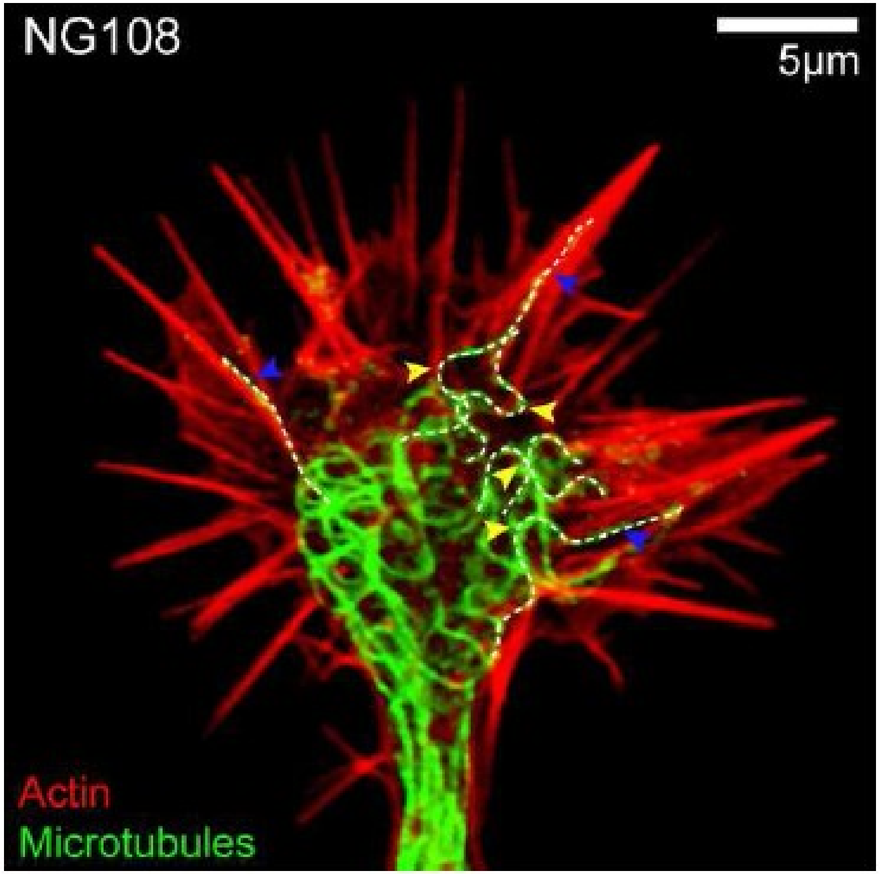
Fluctuation-dissipation ratio

$$R_{q_x \omega} = \frac{N_1 \gamma}{k_B T} \left[1 + \frac{\alpha \left(\alpha N_2 / N_1 + \beta \right) \left(\zeta / K \right)^2 q_x^2 \Sigma(q_\omega)}{1 - \alpha\beta(\zeta/K)^2 q_x^2 \Sigma(q_\omega)} \right]$$

- A mess: should be unity if effective temperature
- Depends on activity through Σ
- Can turn negative at finite frequency
- Close analogy: Hudspeth *et al* PNAS '01 auditory hair cells

Axon growth cone: active softening and stiffening?

Ehrlicher,
Koch,
Kaes 2008



Conclusion

- Framework for mechanics of living matter
- Striking rheology, instabilities; new coarsening
- Active clumping: bio consequences? Madan's talk
- Granular experiments: giant number fluctuations
- Many new directions to be explored

If we shadows have offended
think but this and all is mended
that you have but slumbered here
whilst these visions did appear.....